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Studies on leaf temperature recorded by direct measurement and by thermography

by

Lars Thofelt

UPPSALA 1975

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1976

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Doctoral thesis at Uppsala University 1976
ISBN 91-554-0341-7

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STUDIES ON LEAF TEMPERATURE RECORDED BY DIRECT MEASUREMENT AND BY THERMOGRAPHY.

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ABSTRACT

In vascular plants, the leaves constitute a living exchange system between the plant and its external environment. The effectiveness of this exchange system is dependent largely on temperature; leaf temperature influences many physiological processes among which transpiration may be the most important under ecological conditions because transpiration controls the water content of the plant, which in turn determines the stomatal width and consequently photosynthesis.

A lot of factors influence leaf temperature. Of these, external factors include the quality and quantity of incident radiation, the direction and velocity of the wind, and the micro-climatic conditions of the surroundings. Internal factors depend on genetic and other properties of the leaf.

The influence of external factors on leaf temperature was studied in this work. Laboratory experiments showed that radiation, wind velocity and leaf position were important in determining leaf temperatures. It is suggested that heat is absorbed and translocated by the water in the leaf and in the boundary layer around it.

In the field, it was found that radiation, both solar and terrestrial, was the most important factor influencing leaf temperature. A temperature gradient in the plants existed during the day. At night, a temperature gradient existed in a plant at sea level, but not in a plant in the mountains. Reradiation from the mountain plant was found to be relatively more important.

Thermography was applied to measuring the temperature of plants and found to be a most useful tool, because the thermal picture of the plant, viewed in the monitor, can be studied in minute detail. Relative temperatures of the plant can be exactly determined, but the measurement of the true temperature of a plant is associated with some complications since the reflectivity of the leaves must be considered in calculating true temperature. Since thermography enables a thorough interpretation of the temperature differences in different parts of a plant, it is preferable to one-point methods of measurement with temperature sensors.

In measuring leaf temperature with temperature sensors, it was found that attaching the sensor to the surface of the leaf gave too high a temperature, and inserting it into leaf mesophyll too low a temperature. The repeated touch method was introduced to eliminate these difficulties. While, it did eliminate these difficulties, it was still a one-point method of measurement; therefore, another new method, thermography, was developed. It is clearly superior as a method to measure leaf temperature.

Thermography can advantageously be used to study the thermal response of plants to changes in external and internal factors. In the field, the influence of short time changes in weather conditions, for example, changes in solar radiation intensity due to changes in cloudiness, wind, and humidity can be studied. Longer time changes, for example, shorter day length and lesser solar radiation intensity, can also be effectively studied. Plant response at different locations, humid, arid, temperate, or frigid, can be compared. Thermography can also be used in evaluating the elements in the energy budget concept in experiments with models, dry or wet. Research on this problem has already been described by Wigley and Clark (1974).

In the laboratory, the influence of different chemicals on temperature response of plants, the influence of changing day lengths, dry or wet soil conditions, and the like, can be compared.

Technical development has given the plant physiologist a tool for temperature measurement which makes it possible to measure simultaneously temperatures over the whole plant under different experimental conditions and compare the thermal pattern. The method is rapid and very exact as far as relative temperature are concerned. However, the true temperature of the plant has to be considered relative to the reflectivity and transmissivity of the plant. For short term measurement, at least, thermography is at present the most useful method for measuring the temperature of plants.

CONTENTS

	Page
I. LEAF POSITION, WIND VELOCITY AND IRRADIATION INTENSITY INFLUENCE LEAF TEMPERATURE.	7
Introduction	8
Background	9
Material and Methods	11
Results	19
Discussion	42
References	49
II. THERMOGRAPHIC MEASUREMENTS OF LEAF TEMPERATURE.	53
Introduction	54
Material and Methods	54
Results	56
Discussion	61
References	65
III. THERMOGRAPHIC MEASUREMENTS OF THE TEMPERATURE OF SMALL BIRCHES IN THE FIELD.	75
Introduction	76
Abbreviations and symbols	80
Results	81
Storhogna in July	81
Alnön in July	101
Storhogna in August	121
Discussion	136
References	140
Acknowledgements	142

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LEAF POSITION, WIND VELOCITY, AND IRRADIATION INTENSITY INFLUENCE LEAF TEMPERATURE.

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ABSTRACT

Leaf position affected temperature and transpiration of aspen (Populus tremula) and Hibiscus (Hibiscus sinensis) leaves. High irradiation intensity caused injury to the leaves, most severe when the upper surface of the leaf was irradiated. No injury occurred when the direction of irradiation was parallel to the leaf surface or when wind velocity was at least 0.6 m s^{-1}. The leaf temperature also fell as the leaf dried.

It is suggested that heat radiation is mainly absorbed and translocated by the water of the leaf and by the water vapor of the boundary layer.

INTRODUCTION

In vascular plants, leaves constitute a living exchange system between the plant and its external environment. The effectiveness of this exchange system is dependent largely on temperature; leaf temperature influences many physiological processes among which transpiration may be the most important under ecological conditions because transpiration controls the water content of the plant, which in turn determines the stomatal width and consequently photosynthesis.

The stomata regulate the rate of exchange of gases, primarily carbon dioxide, oxygen and water, which are vital for the growth of the plant. With excessive incident radiation the stomata of the leaf may either close, thus preventing the gaseous exchange vital for photosynthesis, of fully open, thus increasing water losses from the leaf. In either case, survival of the plant may be endangered. Simultaneously, other temperature dependent processes may occur, promoting or detaining the growth of the plant.

As a significant part of the vitally important physiological processes occur in the leaves, and these processes are in one way or another temperature dependent, the temperature of the leaves in different eco-physiological situations is something of a key to the growth response of the plant. Of the factors influencing leaf temperature, one can distinguish between external and internal. External factors include the quality and quantity of the incident radiation, the direction and velocity of the wind and micro-climatic conditions of the surroundings, i.e. temperature and humidity. Also water losses from the leaf influences leaf temperature. The effects of these factors can be studied with simple models such as thin metalplates, papers, etc. or with models made of wet blotting-paper or "multi-perforated septa" (cf Huber 1956). Internal factors depend on properties of the leaf. For example, the temperature of the water flowing into the leaf and to different parts of the leaf and also the water transport capacity between different parts of the leaf are presumably affecting leaf temperature.

This study is an attempt to clarify some of the factors influencing the temperature of aspen (Populus tremula) and Hibiscus (Hibiscus sinensis) leaves. The aim of the study was to help us evaluate the effect of external factors on leaf temperature so that we can better interpret field measurements of temperature. To do this, comparisons of different methods of measuring leaf temperature was necessary.

Background

Theoretical studies and model experiments, often done with thin, flat metalplates cut into different shapes, have been used in order to study heat-transfer mechanisms between leaves and their surroundings. The results have been expressed in mathematical terms which are theoretically valid for living leaves (Gates 1962 b, Gates and Papian 1971, Knoerr and Gay 1965, Raschke 1956).

The temperature of living leaves reaches a steady-state condition under constant irradiation (Kleshnin and Shul´gin 1958). Temperature differences between leaves increases with increasing irradiation as does transpiration (Salisbury and Spomer 1964). Both temperature and variation in temperature depend on the water content of the leaf, its position and the distribution of irradiation (Ansari and Loomis 1959, Dörr 1941, Kleshnin and Shul´gin 1958, Konis 1950, Salisbury and Spomer 1964, Shull 1936). The temperature of thicker leaves stabilized more slowly than that of thinner leaves, whether irradiated (Shull 1936) or shaded (Ansari and Loomis 1959, Baskin and Baskin 1971, Curtis 1936, Mellor et al 1964, Kleshnin 1951) and water losses from leaves result in decreases in leaf temperature (Kleshnin 1951).

Dry artificial leaves subject to increasing irradiation also reach a steady-state condition of "leaf temperature" (Aston et al 1969). Leaf models, made of wet and dry cambric material, dead yellow leaves and green leaves gave similar results (Kleshnin and Shul´gin 1958). With increasing irradiation, the temperature of dry models, made of black paper cut into squares, increased (Curtis 1936). The theoretical computation of the convection of heat between dry, broad artificial leaves and air were confirmed in experiments in a windtunnel (Parkhurst et al 1968). Dry models of broad leaves are warmer than dry models of needles both in still air and wind (Tibbals et al 1964). As more pores per area increases, evaporation from "multi-perforated septa" increases (Huber 1956).

Reradiation, transpiration, and convection are important processes in reducing leaf temperatures (Gates 1962 a) with reradiation considered the most important (Ansari and Loomis 1959, Curtis 1936, Gates 1963, Raschke 1956, 1960), especially in dry air (Curtis 1936, Linacre 1965). However, leaf temperature and transpiration are "tied inexorably together through the energy budget for the leaf" according to Gates (1968). Cal-

culations show that "transpiration must play a major role in maintaining leaf temperature below lethal values" (Gates 1962 b). Convection is considered of minor importance in reducing leaf temperature (Cook et al 1964, Gates 1962 b) but with increasing wind velocity, its significance increases.

Variation of leaf temperature at different points of the leaf blade has long been known to exist (Kleshnin and Shul'gin 1958). These variations in tomato leaves have been explained as differences in transpiration (Cook et al 1964), the midpoint of the leaf being consistently cooler than the edges (Ullrich and Mäde 1938).

The radiation regime, the genetic make up of the plant, water status of the soil, and time of the year all influence the spectral properties of the leaves (Billings and Morris 1951, Dadykin and Bedenko 1960, 1961, Tageeva et al 1960) and hence leaf temperature. Small leaves absorb less and loose more heat than broad leaves. The length of the edges of the leaf compared with the area of the leaf is directly related to heat losses of the leaf. The increases of this ratio reduces the thickness of the boundary layer and consequently heat losses from the leaf through reradiation increases. This has been shown in model experiments (Raschke 1960, Seybold 1927). Schanderl (1932) found that leaves of Lactuca scariola were more laciniated where heat radiation was more intense. Taylor and Sexton (1972) were able to show dramatic drop in temperature of frayed banana leaves as compared with the temperature of intact banana leaves.

Previous work on leaf temperature has been reviewed by Lange (1965) and by Perrier (1971). In recent studies the recording has usually been done with thermoelectric methods using thermocouples or thermistors as temperature sensors. Good contact between the sensor and the leaf has been achieved by inserting the sensor into the leaf mesophyll (Ansari and Loomis 1959, Baskin and Baskin 1971, Cook et al 1964, Gates 1964, Kleshnin 1951, Mellor et al 1964, Salisbury and Spomer 1964, Vaupel 1958) or by attaching it to the leaf surface (Gale et al 1970, Lange 1959, 1965, Lange and Lange 1963, Shull 1936, Ullrich and Mäde 1938), the former method usually being employed. In either method, however, the heat transfer processes themselves are probably affected. The insertion-caused wounding may change biochemical processes. The temperature of the wound has been observed to be lower than that of the surrounding leaf blade (Thofelt 1975 b).

If the temperature sensor is placed on the shaded surface of the leaf, the recorded temperature is presumably too high because heat is transmitted via the water of the leaf through the leaf to the attached sensor. The surface of the leaf and the attached sensor forms a sort of "closed chamber", which accumulates heat. If the sensor is attached to the irradiated surface of the leaf, the shading effect results in too low a temperature recording.

The solar constant, or the extraterrestrial solar radiation, is 1395 joule m^{-2} s^{-1} (Johnson 1954), with 98 % in the wavelength-band 0.5 - 4.5 µm and about 40 - 45 % in the visible wavelength-band (Slatyer 1967). At the surface of the earth about 29 % of the solar radiation is in the wavelength-band above 1 µm and about 50 % above 0.78 µm (Gates 1962 a). Water and carbon dioxide molecules, and to a smaller degree also oxygen and ozone molecules, absorb radiation in certain wavelength-bands above 1 µm (Gates 1962 a). The absorbed radiation is reradiated as heat (Gates 1962 a, Schanderl 1932, Vaupel 1958). Reradiation of heat from plants has maxima at 8.9 and 10.5 µm (Raschke 1956, 1960). The emissivity of leaves is between 0.97 - 0.98 or very near unity (Gates and Tantraporn 1952). They can, for practical purposes, be regarded as black bodies.

In the visible wavelength-band reflectance, transmittance and absorption of radiation have been investigated by Kleshnin and Shul'gin (1959). The reflectance of plants was about 50 % in the wavelength-band 0.78 - 1.1 µm (Billings and Morris 1951). The reflectance of leaves in the infrared beyond 2.0 µm is small, about 5 % (Gates and Tantraporn 1952, Wong and Blevin 1967); "the upper surface reflects more than the lower, old leaves more than young, and the shade leaf more than the sun leaf" (Gates and Tantraporn 1952).

MATERIAL AND METHODS

Aspen and Hibiscus leaves were used in the experiments. Aspen leaves are excellent for leaf temperature investigations because they are circular, simple, stiff, and have a long petiole. Hibiscus leaves were used when aspen leaves were not available. The mean area for aspen leaves was 18.8 cm^2 and for Hibiscus leaves 27.4 cm^2, measured as recommended by Polster and Reichenbach (1958).

The petioles were cut under water and each was put between the two halves of a cork (cut lengthwise along a hole of the right size to accomodate the petiole) so that about 2 to 5 cm of the petiole projected beyond the bottom of the cork. Each cork, with its enclosed petiole, was then used to stopper a test tube (about 10 x 55 mm) filled with distilled water. The leaf was placed in darkness for 60 minutes before being used in the experiments.

Water loss from leaves placed in different leaf positions was estimated with a differential psychrometer. The cuvette was made of polyacrylate (figure 1). The air movement through the cuvette was approximately 35 dm^3 h^{-1} or 0.4 cm^3 s^{-1}. The leaf positions used are shown in figure 2.

The stomatal apertures of aspen leaves that had been placed in different leaf positions and irradiated at different intensity levels were measured with an ocular micrometer from gelatine imprints taken from the lower surface of the leaf. Household gelatine was cut into small pieces about 1 cm square. A drop of water was placed on one of these squares and allowed to remain there for about half a minute and then shaken free, and the moistened gelatin was pressed against the leaf and placed on a glass slide for microscopic examination. All the stomata in each of several fields of view, until at least 48 stomata had been counted, were observed. Relative size of the stomatal openings is recorded in figure 17, with the stomatal aperture size of the position 3 leaves as 100 percent (1.0), cf Froeschel 1961.

In order to avoid possible errors in measuring true leaf temperature, caused by wounding when the temperature sensor is inserted into leaf tissue, or due to the "closed chamber" effect when the sensor is attached to the leaf surface, the "repeated touch" method was developed. The construction of the sensing probe is a critical feature of this method. The thermocouple was mounted on the middle and largest prong of a three prong probe with the four thin connecting wires attached to the side "prongs" which were elongated parallel to each other (see figure 3). The handle of the probe was insulated. The probe is brought into contact with the leaf for about one second and the temperature recorded. This process is repeated four to six times at intervals of about one second and the mean temperature is calculated. In routine work the difference between one reading and the next is about 0.2°C at moderate levels of irradiation (below 1500 joule m^{-2} s^{-1}).

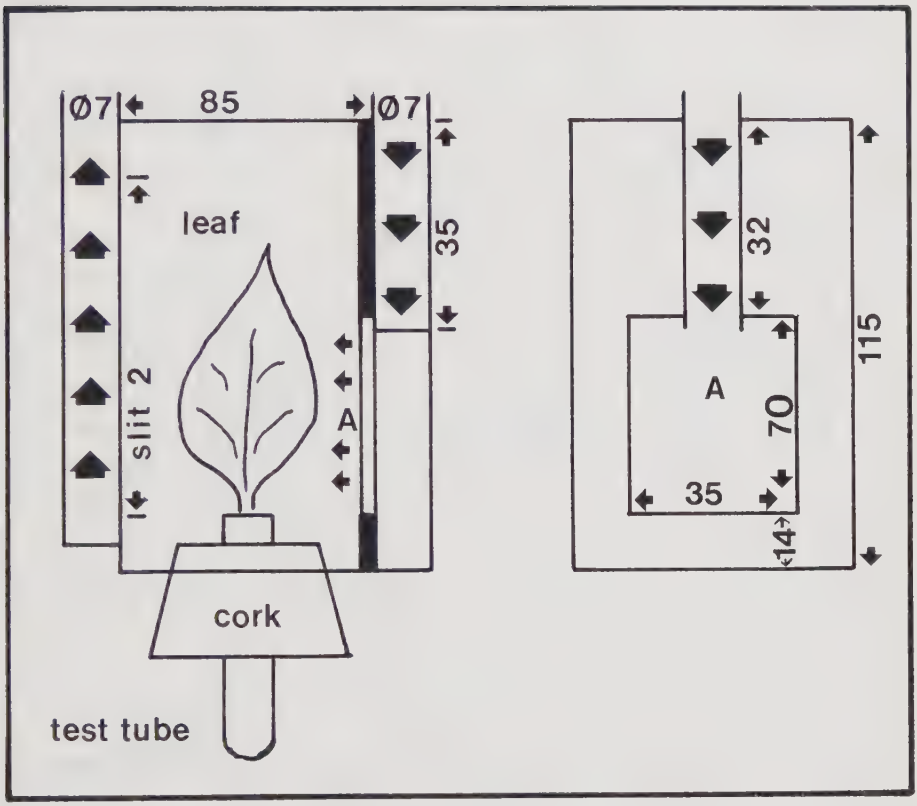


Figure 1. The cuvette. Left: side view. Right: seen from the direction and wind. Measurements in mm. Area A had 72 x 1 mm and 5 x 2 mm holes made to give an evenly distributed air flow over the leaf blade.

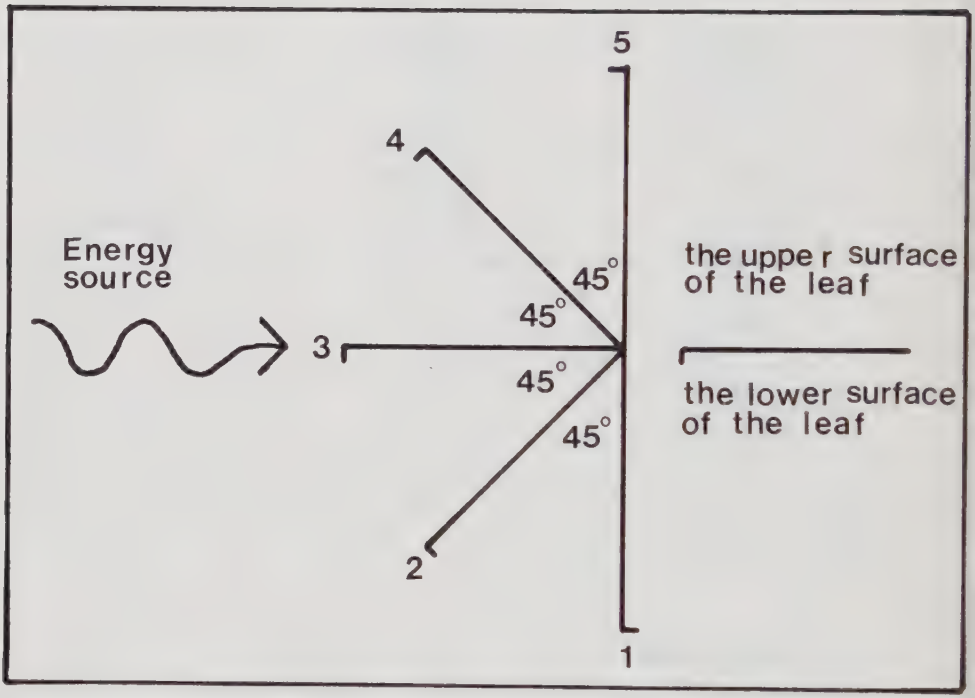


Figure 2. The leaf positions used.

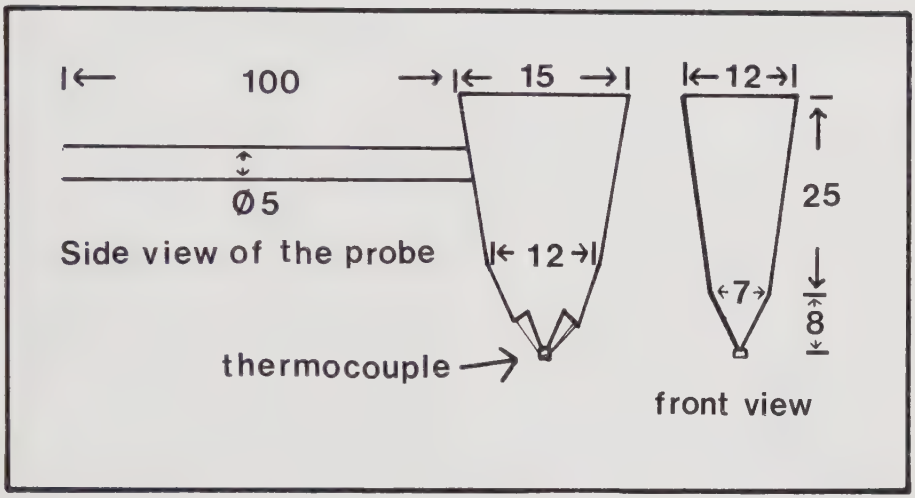


Figure 3. The mounting of the thermocouple on the probe. Measurements in mm.

The temperature sensor was a non-corrosive thermocouple made of Ni/NiCr. The reference temperature was obtained with a Dewar flask containing a water-ice mixture. The water-ixe mixture was periodically stirred. Radiation was measured with a silicone photovoltaic cell (TP61 made by Siemens). Wind was measured with a hot-wire anemometer (Thermoelektrisches Hitzdrahtanemometer, Fuess, Berlin) just above the leaf. The equipment was battery driven.

The energy sources used, generally one at a time, with a colour-temperature of 2700 K, were incandescent lamps (Type 13011, Philips, Holland), see figure 4. A windtunnel (diameter 196 mm, total length 760 mm), with wind capacities between 0.1 and 0.7 m s^{-1}, was used.

Preliminary experiments showed that the leaf temperature was not the same all over the leaf surface (figure 5). The temperature at 2 to 4 mm from the edges of the leaf was usually greater than at the centre, in accordance with investigations by Cook et al (1964) and Ullrich and Mäde (1938). Consequently, leaf temperature was always measured adjacent to the mesophyll tissue on each side of the central vein at the midpoint of the leaf.

If the sensor was left attached to the shaded side of the leaf, the temperature increased very rapidly. If it was left attached to the irradiated side of the leaf, the temperature decreased.

The air surrounding the leaf was measured by moving the sensor parallel to the leaf surface at a distance of one to two mm over its central part. There were no increases in temperature, like those measured when the temperature sensor touched the leaf surface during the measurements of air temperature. In the course of an experiment the measurements were always made in the following order:

air temperature of the shaded side,
leaf temperature of the shaded side,
leaf temperature of the irradiated side,
air temperature of the irradiated side.

The leaves were placed in different leaf positions in the cuvette with irradiation and air movement flowing in the same direction ("A" in figure 1). Because of the experimental conditions unique for the particular cuvette used in the transpiration measurements, which makes absolute values of transpiration measurements relevant only for the cuvette in question, the results are here expressed as differences to the instrument reading at the start of the experiment.

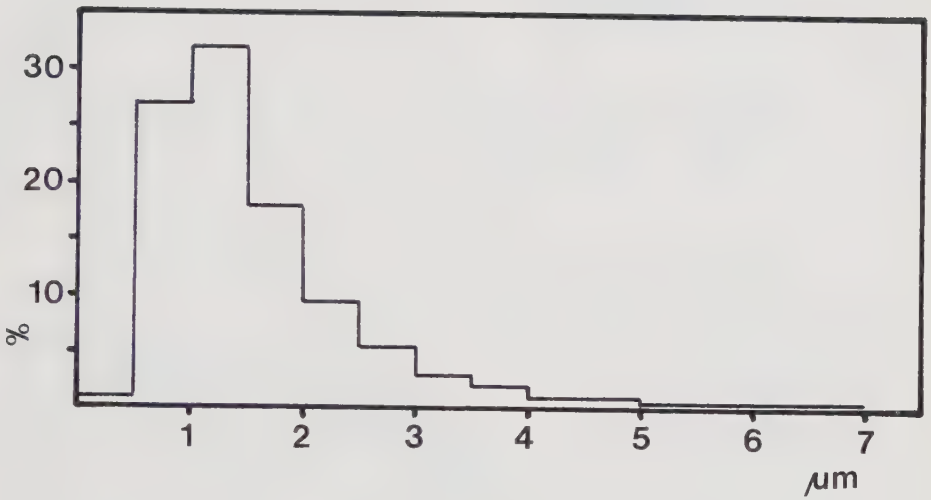


Figure 4. The spectral distribution of radiation from the Attralux incandescent lamp. Colour temperature 2700 K.

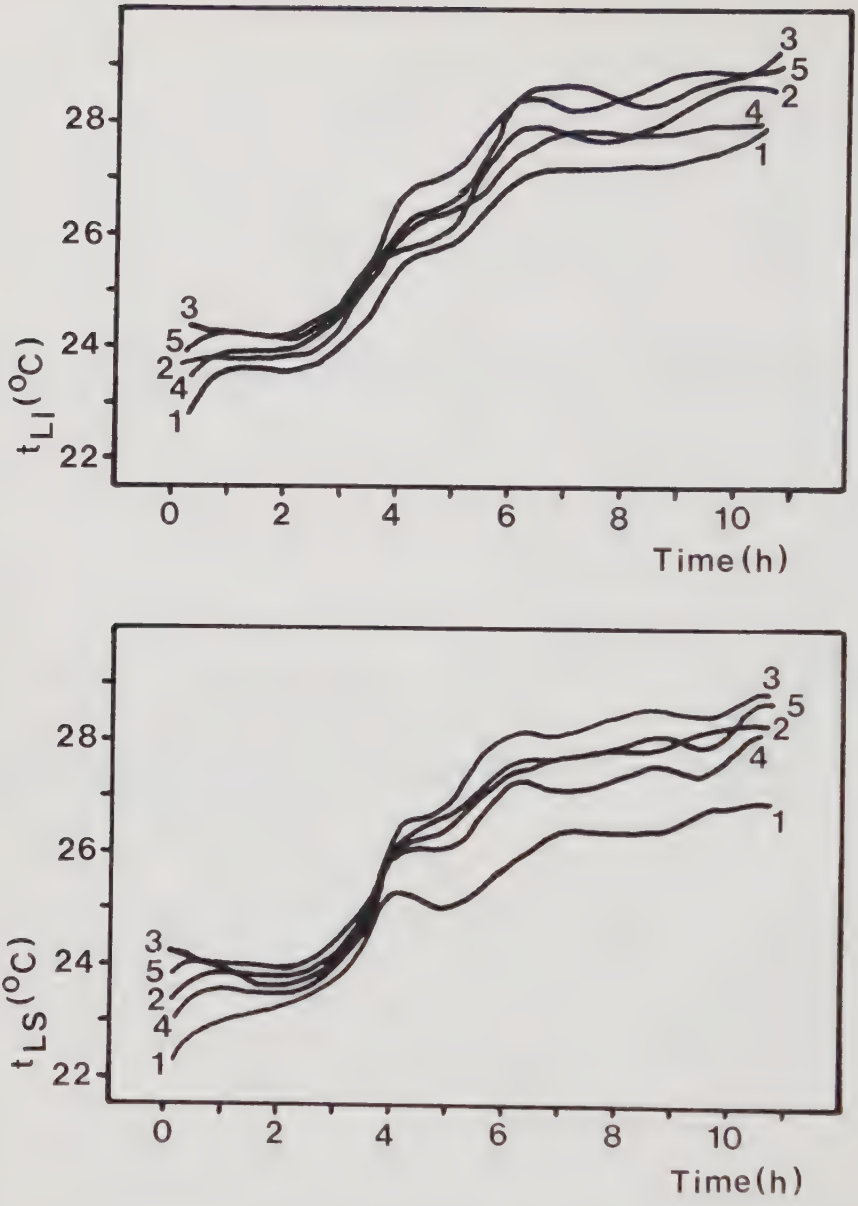


Figure 1. The effect of irradiation on leaf temperature at different points (1 - 5) of an Aspen leaf placed in leaf position 1. Incident radiation 150 joule s^{-1} m^{-2}, wind velocity 1.2 m s^{-1}. Points 1 to 5 are along the midvein of lower, proximal and apex, respectively, and points 3 and 4 are at the left and right margins of the leaf (as seen from underneath). Points 3, 4, 5 and 2 were 2 - 4 mm from the edge of the leaf. All measurements made by repeated touch method.

RESULTS

In figures 6 - 18, the following abbreviations are used:

t_{LI}	temperature of the irradiated surface of the leaf in ^{o}C,
t_{AI}	temperature of the adjacent air of the irradiated surface of the leaf in ^{o}C,
t_{LS}	temperature of the shaded surface of the leaf in ^{o}C,
t_{AS}	temperature of the adjacent air of the shaded surface of the leaf in ^{o}C,
$\bar{t}_{LI}$, $\bar{t}_{AI}$, etc.	the mean values of temperature as above in ^{o}C,
t_{L_1}, t_{A_1}, etc.	temperature of the leaf and of the adjacent air of the leaf placed in position 1, respectively, etc.,
I	irradiation in joule m^{-2} s^{-1},
W	wind velocity in m s^{-1}.

In the main experimental series, leaf temperature was recorded from the onset of irradiation until it attained a constant value or until injury was observed. Figure 6 is an example of an experiment in which leaves were irradiated at a high energy level. As the angle of irradiation increased, the temperature increased and became almost constant. Differences of about $2^{o}C$, often less, were observed between successive temperature measurements. Apparently, the temperature of an irradiated leaf never remains constant. Local variations probably occur because of air movement, initiated by irradiation or wind.

The influence of increasing radiation on the temperature of leaves placed in leaf position 1 and 5 is shown in figure 7. Leaves in leaf position 5 had lower temperature than leaves in leaf position 1. This temperature difference, and also the difference between leaf temperature and temperature of adjacent air, increased with increasing irradiation. Irradiation levels of about 1667 joule m^{-2} s^{-1} had the greatest effect on the temperature of the leaf.

The influence of increasing wind velocity on the temperature of leaves placed in leaf position 1 is shown in figure 8. After 90 minutes of experimentation, only the leaves placed in air movements greater than 0.4 m s^{-1} survived.

A summary of the effect of wind, irradiation, and leaf position is presented in figures 8 - 11, respectively. Leaf temperature, measured 60 minutes after the commencement of irradiation, is plotted against

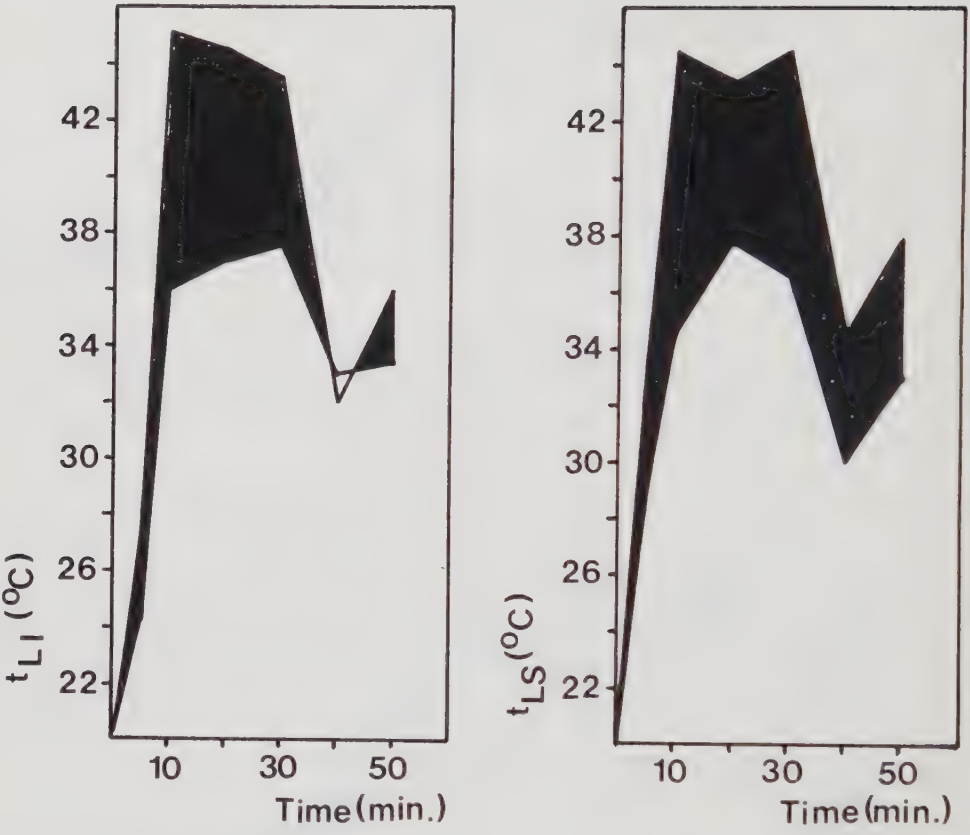


Figure 6:A. The effect of irradiation on the temperature of Gaillardia leaves and of the air near the leaves. The upper curve (exception: figure 6:F) represents leaf temperature and the lower curve the temperature of the ambient air. Mean leaf temperature is greater than air temperature. The area between the curves has been shaded.
Incident radiation (I) : 1317 joule m^{-2} s^{-1}, except for the leaf in position 3 where I = 750. Wind velocity = 0 m s^{-1}.
Figure 6: A - F leaf in position 1 - respectively.

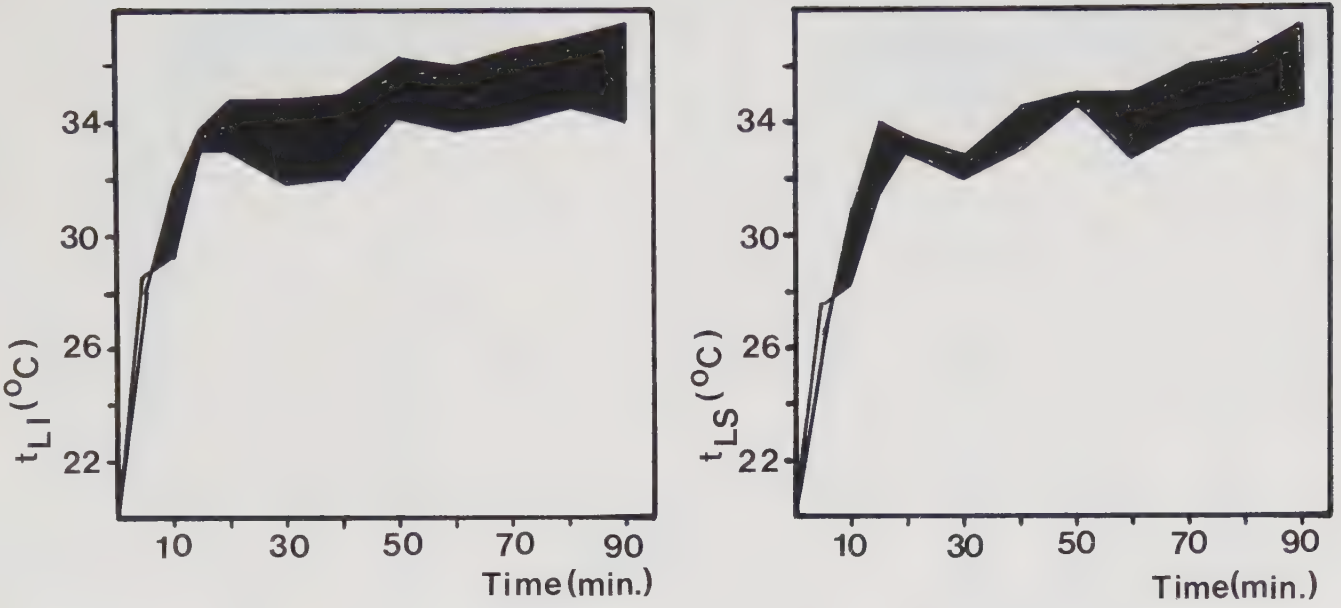
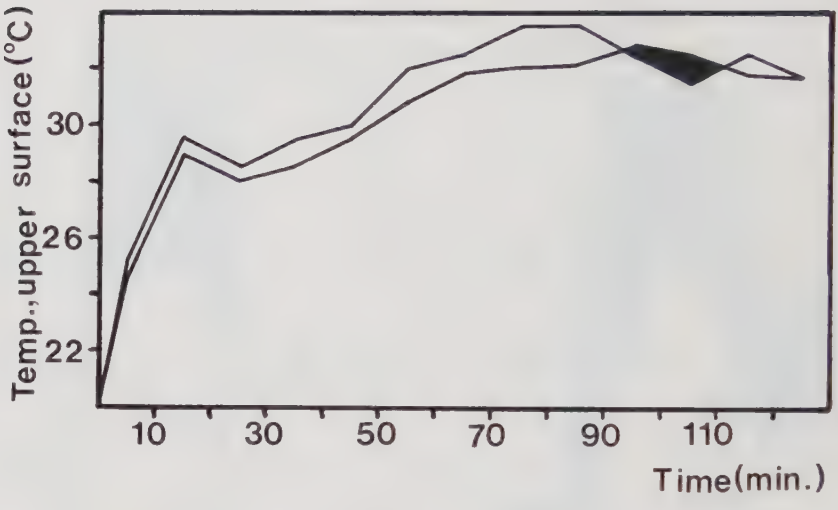


Figure 6:B. Text see fig. 6:A.


Temp.,upper surface(°C)
30
26
22
10
30
50
70
90
110
Time(min.)

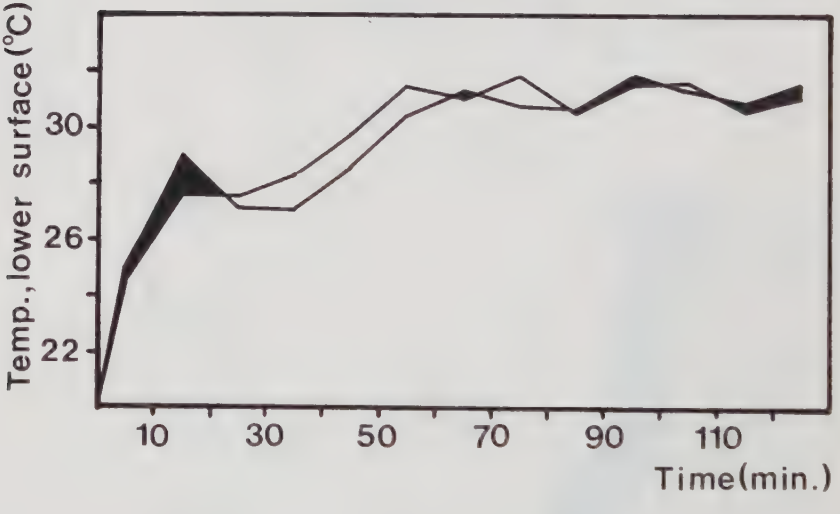

Temp.,lower surface(°C)
30
26
22
10
30
50
70
90
110
Time(min.)

Figure [illegible]

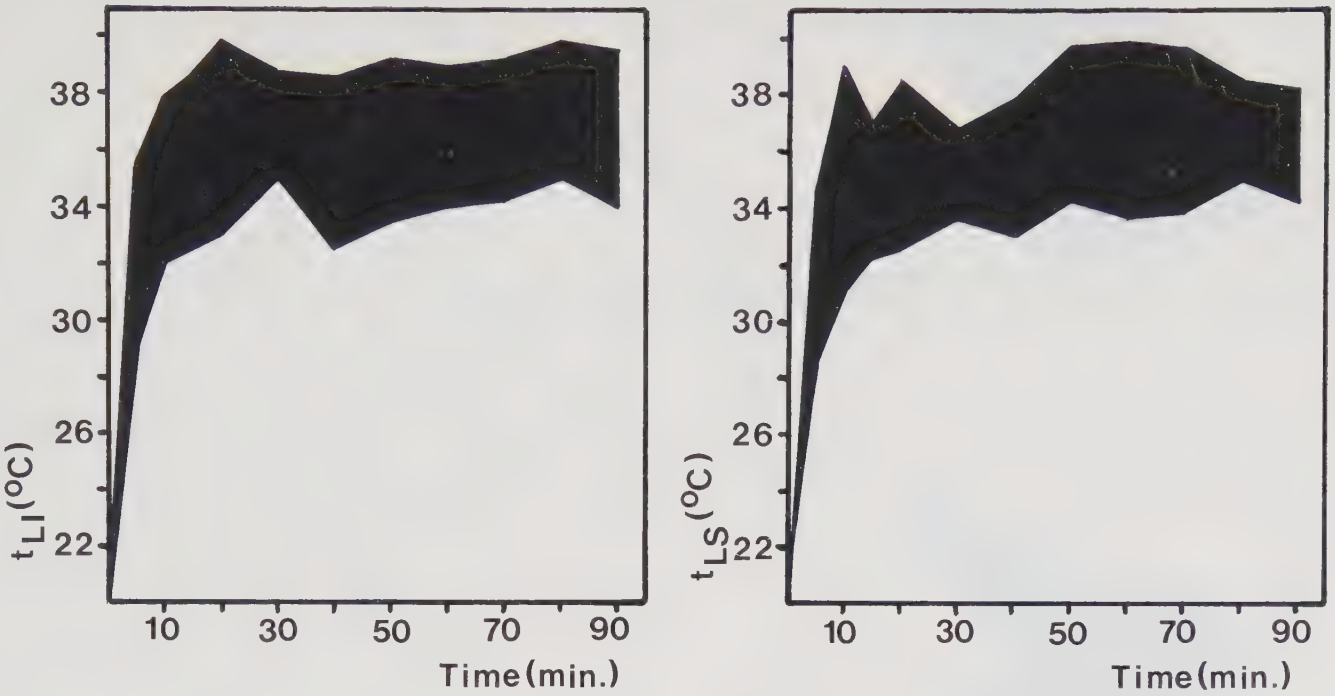


Figure 6:D. Text see fig. 6:A.

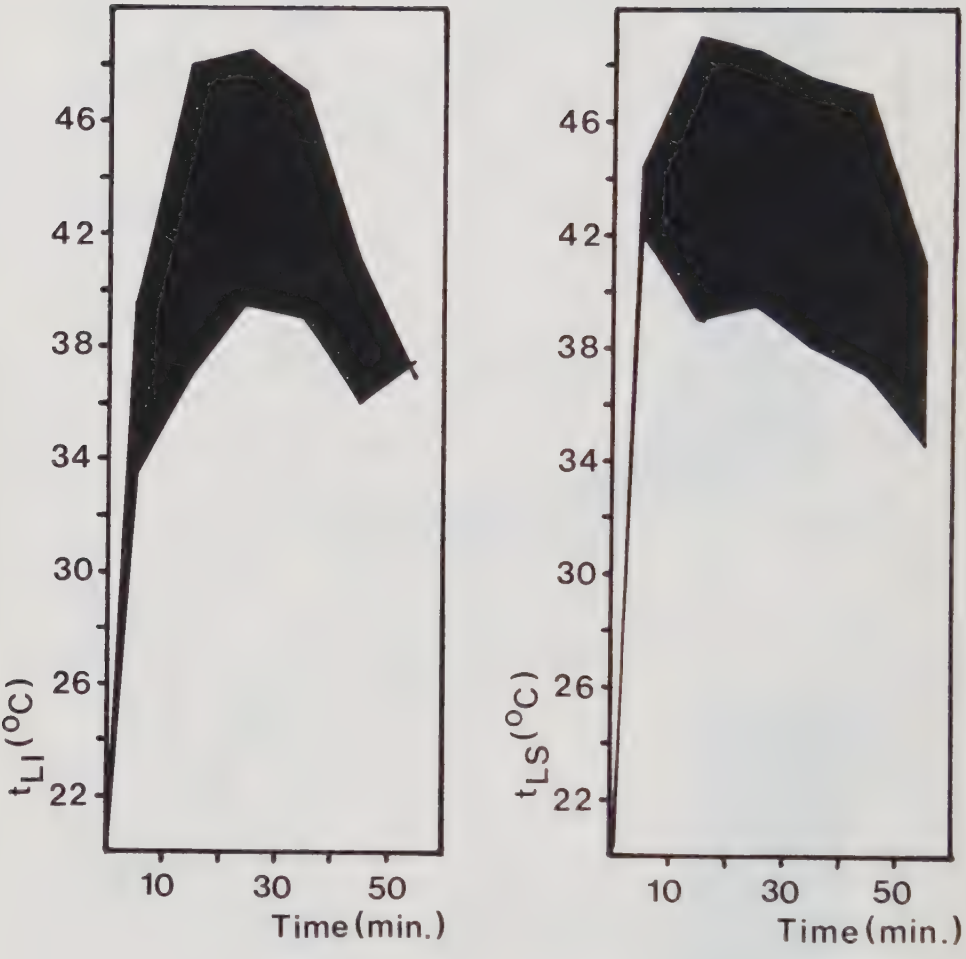


Figure 1:B. Cont. from Fig. 1:A.

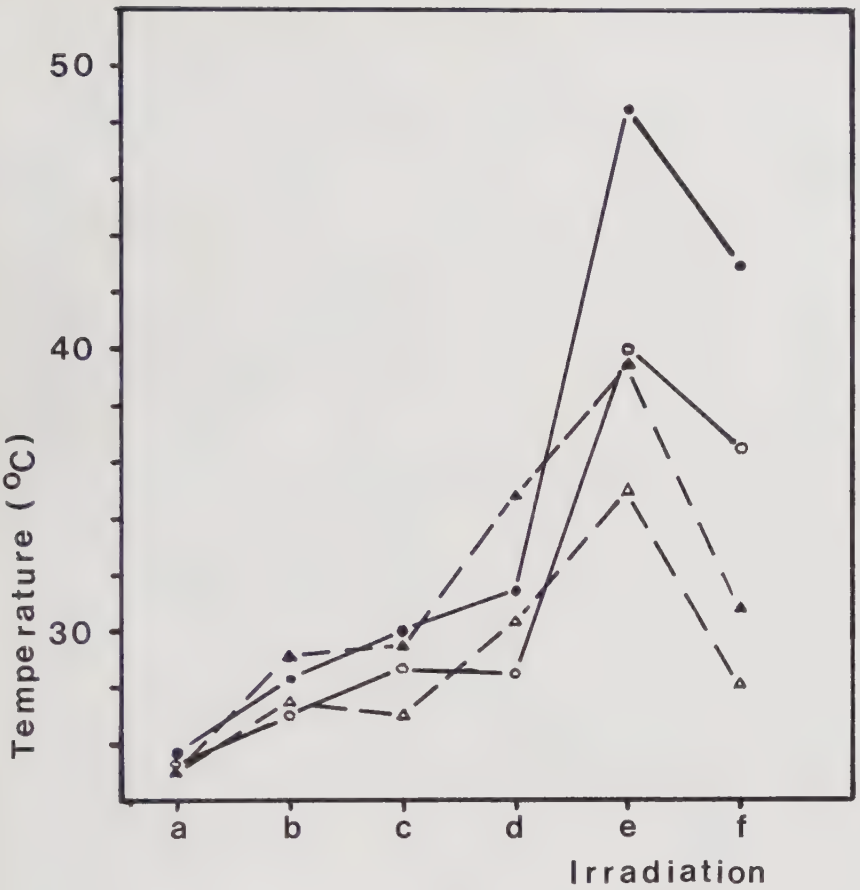
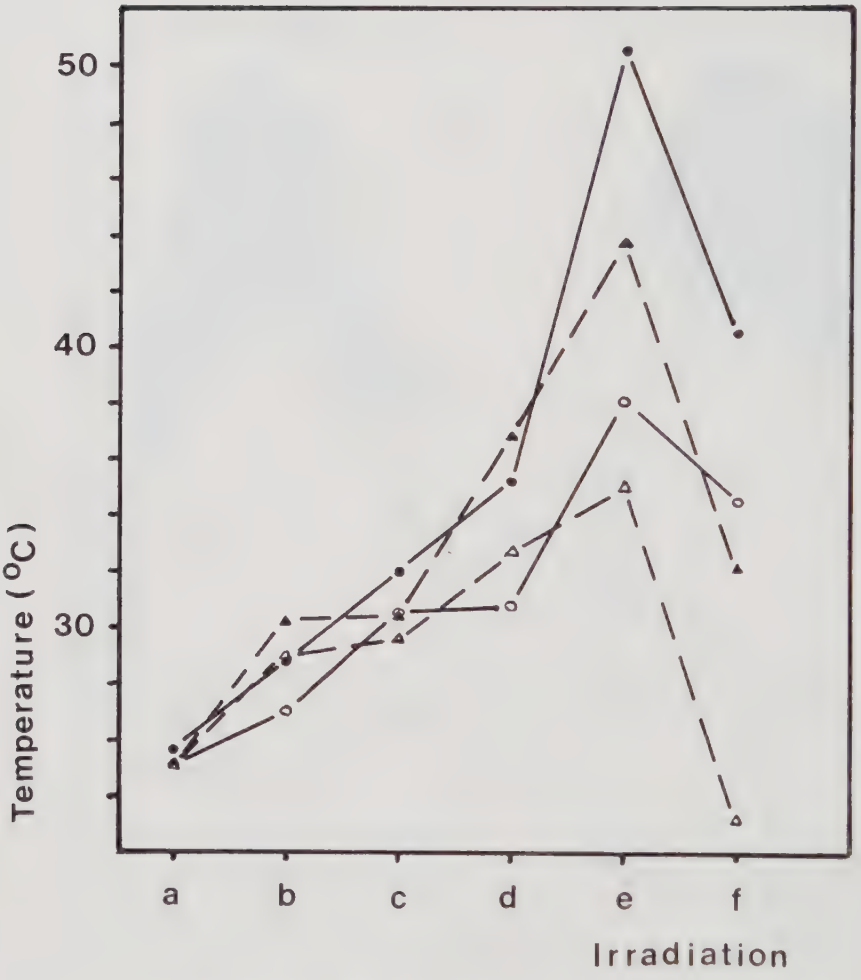


Figure 7:A. The effect of increased intensity of irradiation on the temperature of aspen leaves and on the temperature of the air near the leaves. The temperature of the leaf and of the adjacent air on the irradiated surface of the leaf, figures 7:A and 7:C, on the shaded surface of the leaf, figures 7:B and 7:D. 7:A,B after 15 min.; 7:C,D after 90 min.
(• —— •) t_{L_1}, (o —— o) t_{A_1}; (▲----▲) t_{L_5}, (△----△) t_{A_5}.
a - f represent irradiation levels (joule m^{-2} s^{-1}) of the leaf in position 1 and 5, cf below:

Leaf in	a	b	c	d	e	f
position 1	283	583	783	1350	1667	2000
"- 5	283	500	800	1367	1750	2167



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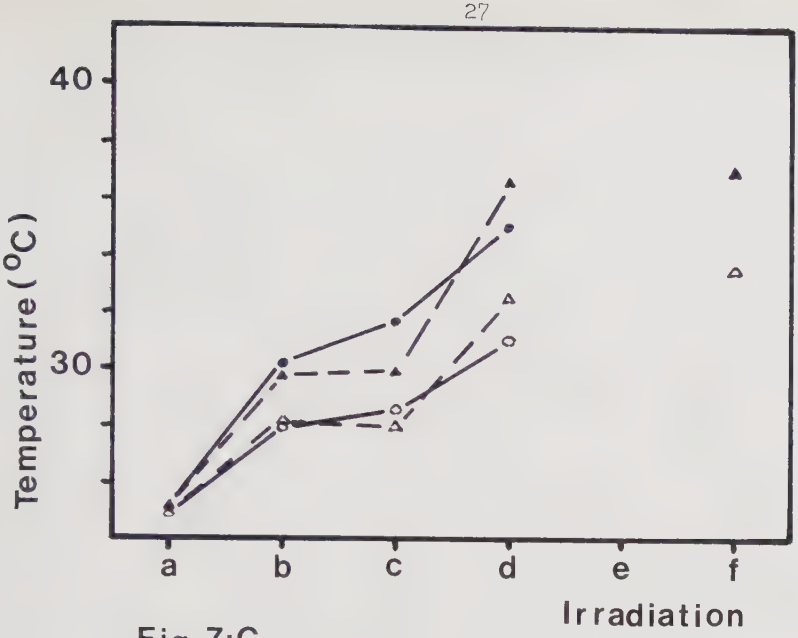


Fig. 7:C

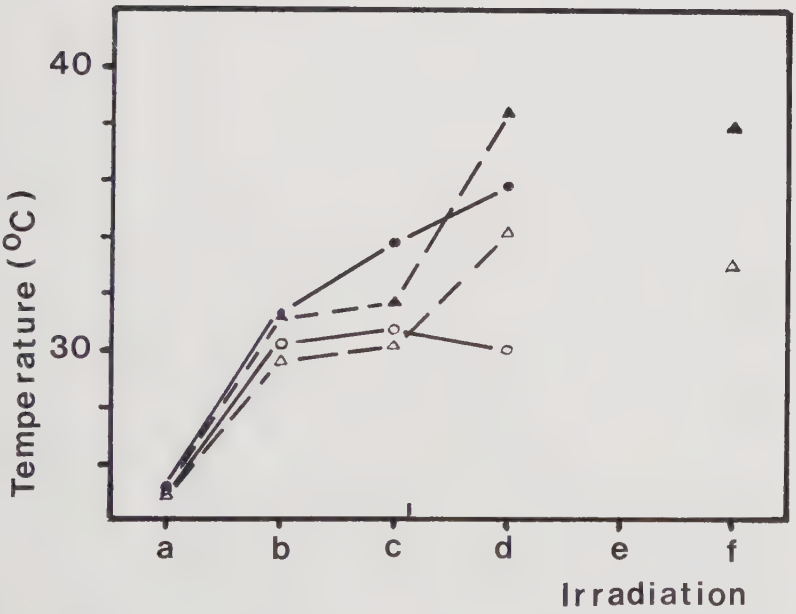
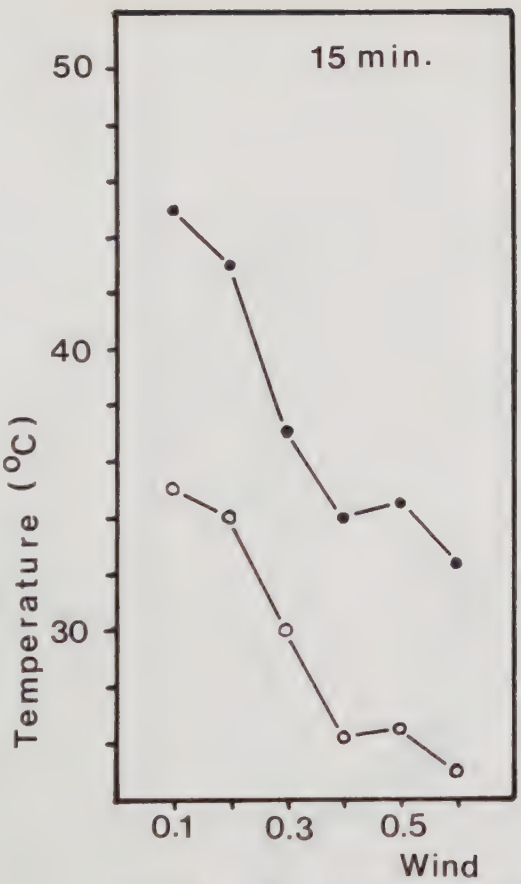


Figure 7:D. Text see fig. 7:A.



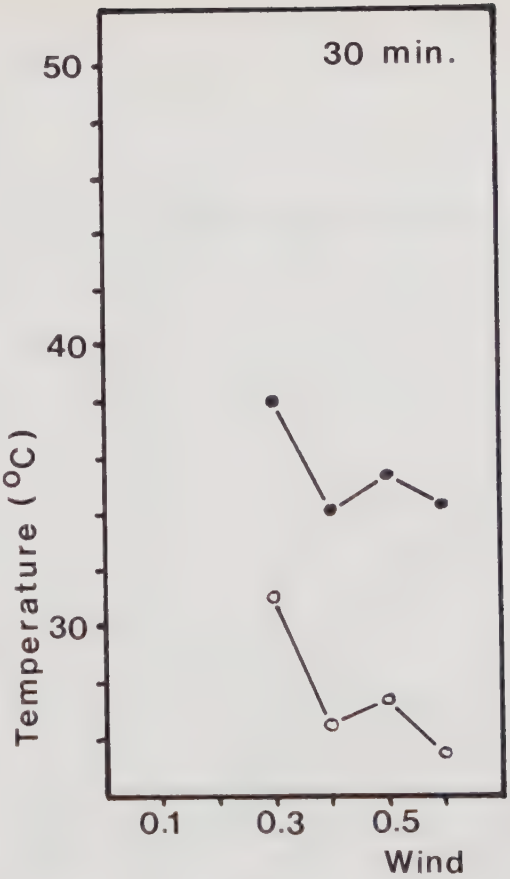


Figure 7:A. The effect of increased wind velocity on the temperature of aspen leaves and of the air near the leaves. The temperature of the leaf and of the adjacent air on the irradiated surface of the leaf, figure 8:A, on the shaded surface of the leaf, figure 8:B. The leaves were placed in position 1. (• —— •) t_{LI}, (o —— o) t_{AI}, (▲----▲) t_{LS}, (△----△) t_{AS}. Irradiation intensity [illegible], [illegible], [illegible], [illegible], [illegible] for wind velocities 0.1, 0.2, 0.3, 0.4, 0.5 and 0.6 respectively.

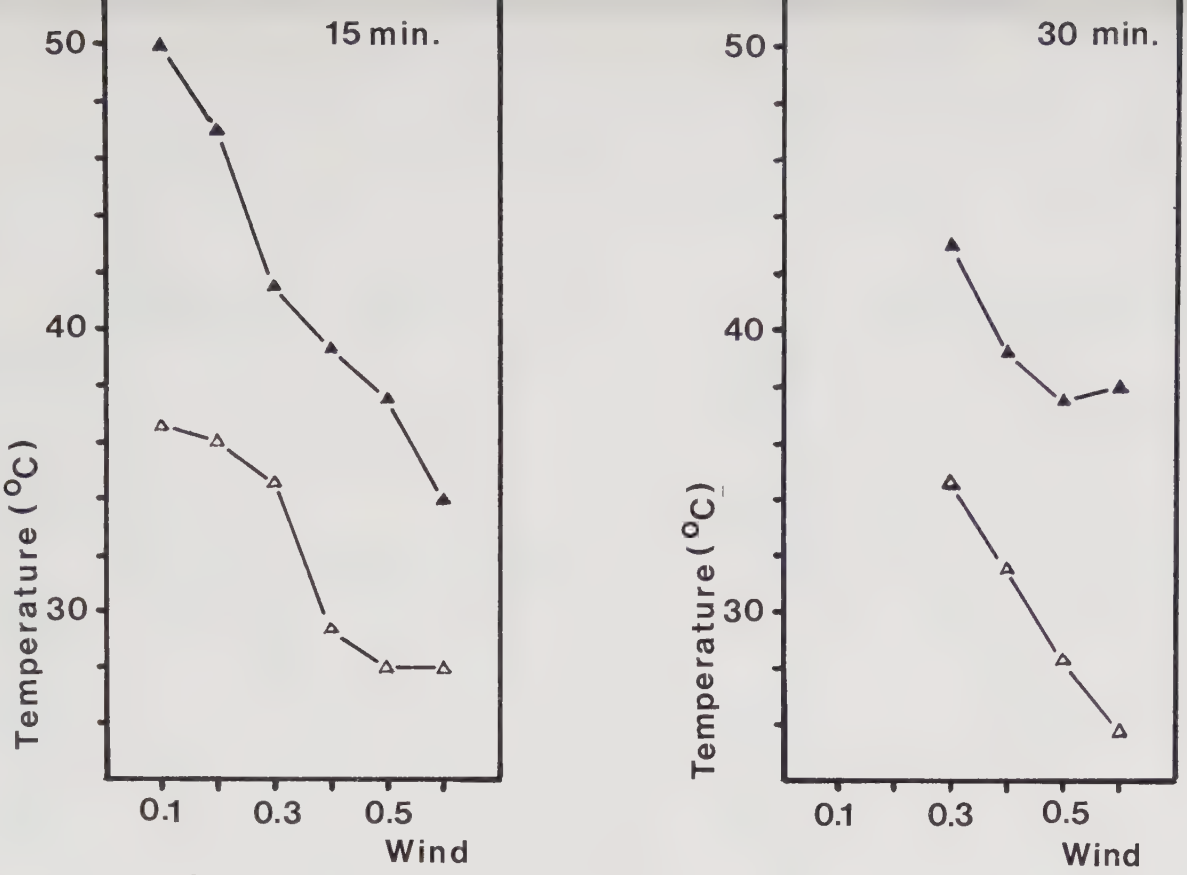
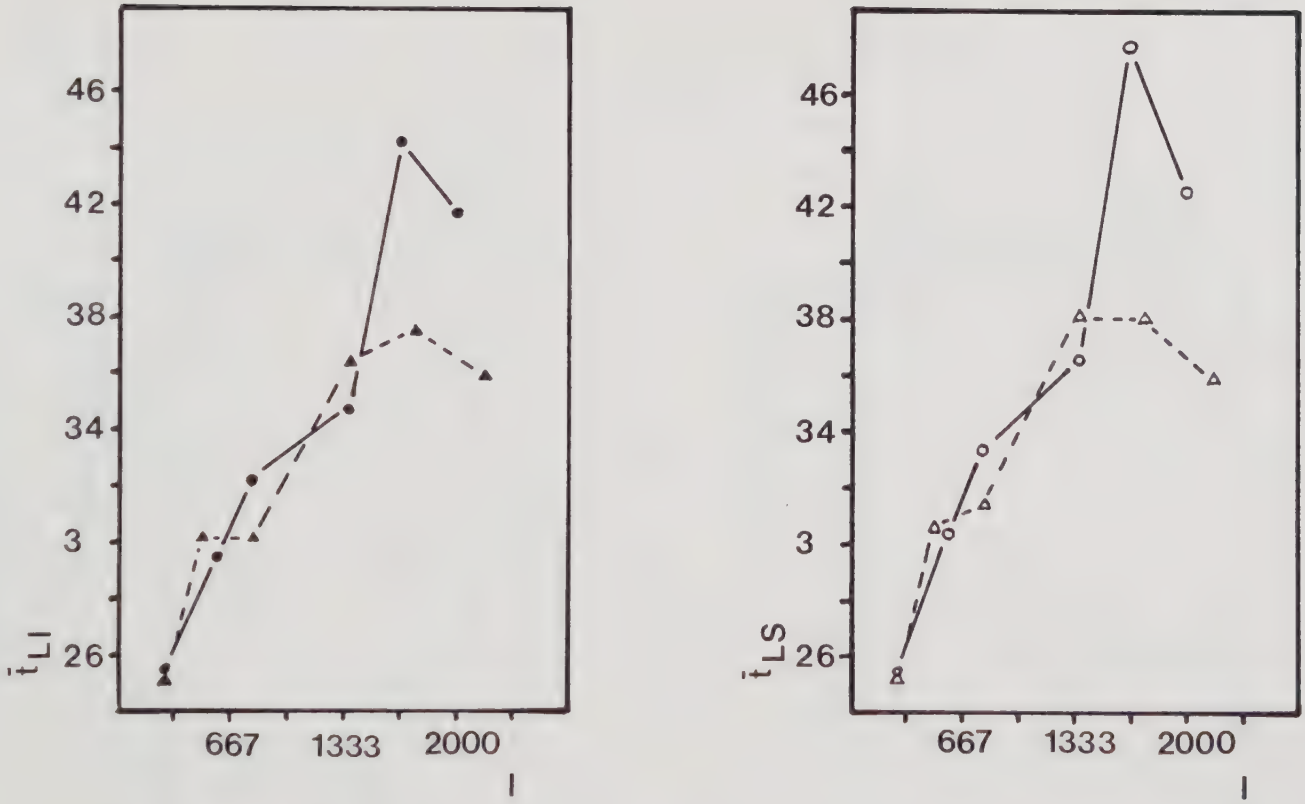


Figure 8:B. Text see fig. 8:A.



... on the temperature of aspen leaves. W = 0.

(•——•) t_{LI}, (○——○) t_{LS}, for leaves in position 1,

(▲----▲) t_{LI}, (△----△) t_{LS}, for leaves in position 3.

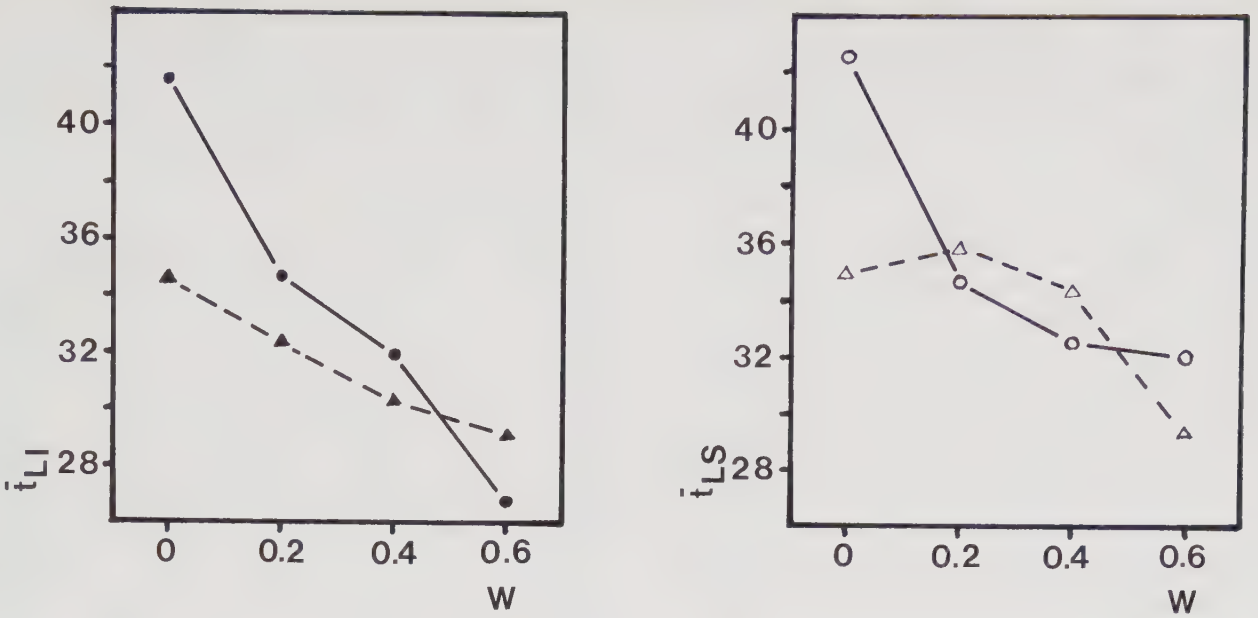


Figure 10. The effect of wind velocity on temperature of aspen leaves. (• —— •) $\bar{t}_{LI}$, (o —— o) $\bar{t}_{LS}$ for leaves in position 1; (▲----▲) $\bar{t}_{LI}$, (△----△) $\bar{t}_{LS}$ for leaves in position 5. Irradiation intensity and wind velocity, see below:

Leaf	W	0	0.2	0.4	0.6
position 1	I	2000	2000	2105	1856
"- 5	I	2167	2105	2000	2250

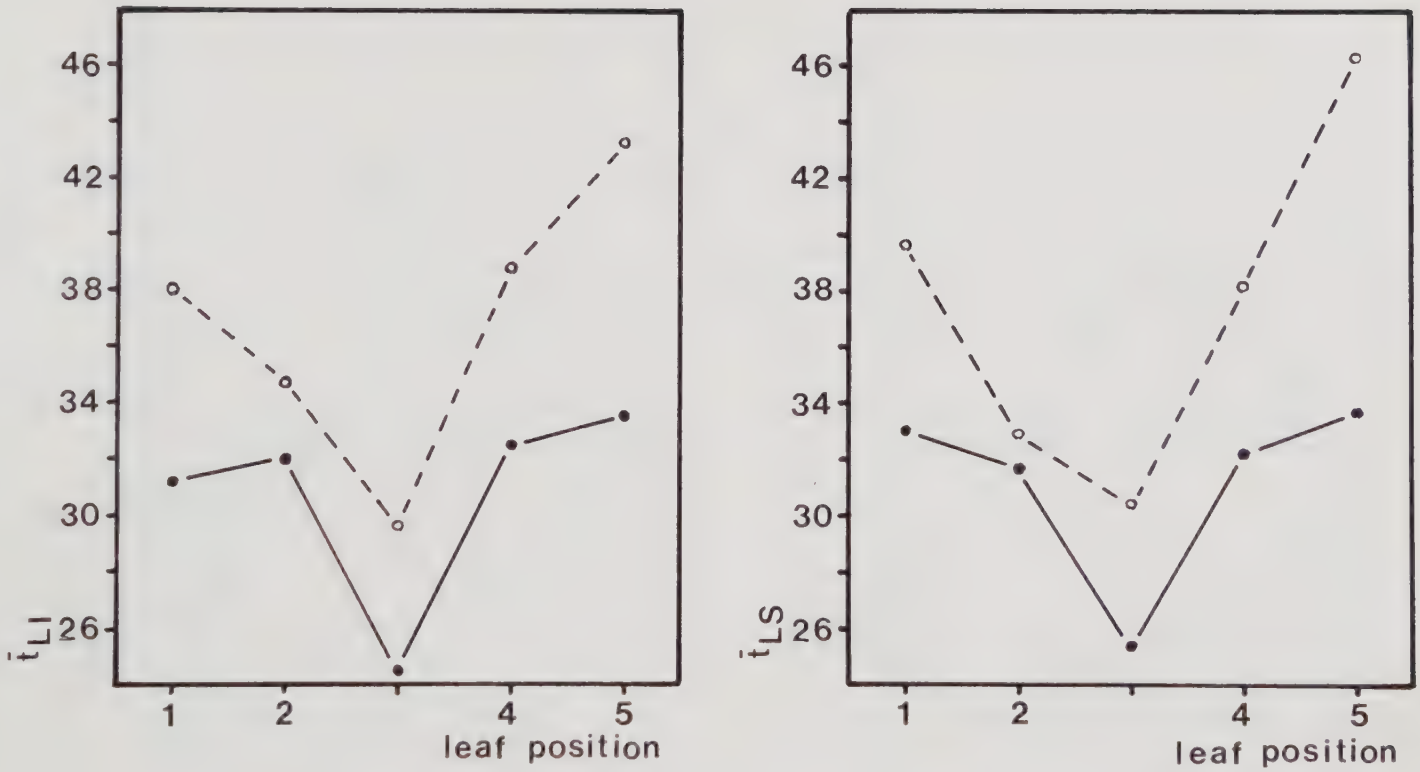
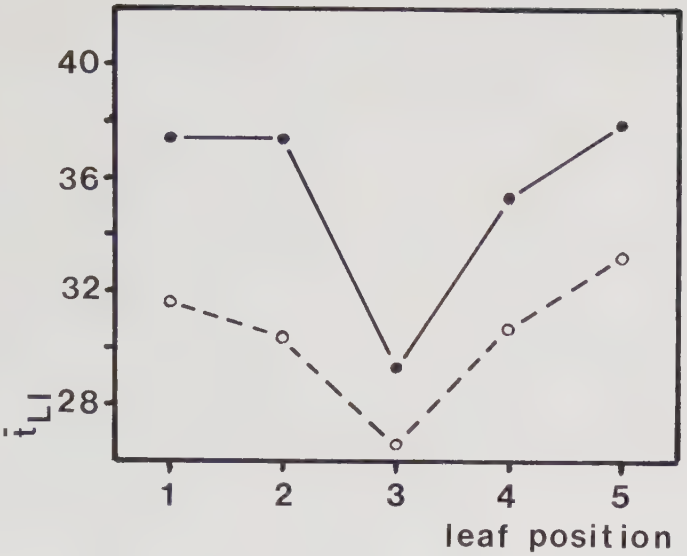


Figure 11:A. The effect of leaf position on temperature of Hibiscus leaves at different irradiation



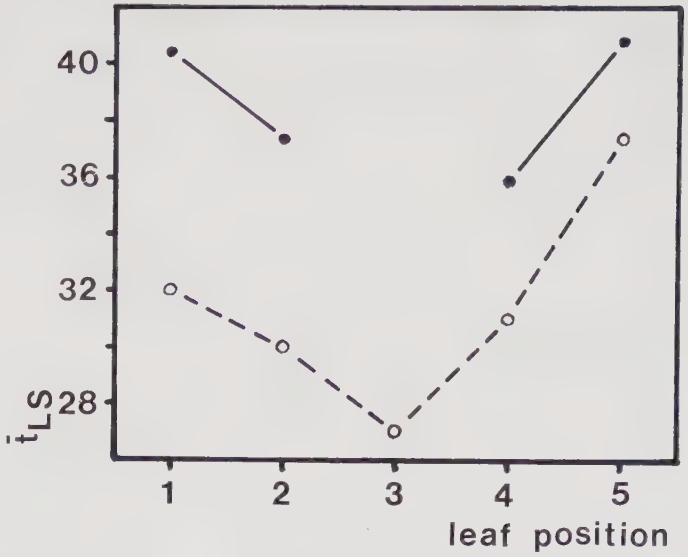
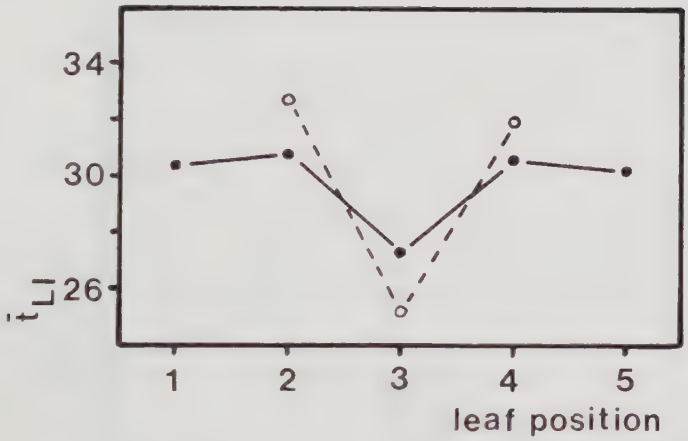
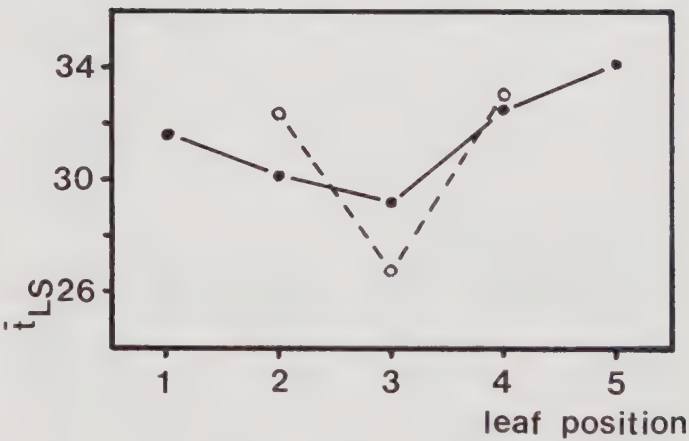


Figure 11:B. Text sec fig. 1..a.


34
30
26
$\bar{t}_{LI}$
1
2
3
4
5
leaf position


34
30
26
$\bar{t}_{LS}$
1
2
3
4
5
leaf position

the manipulated factor. As a rule, the shaded surface attains a higher temperature than the irradiated surface, irradiation of the upper surface causes a greater increase of temperature than the irradiation of the lower surface at high irradiation levels (greater than 1667 joule m^{-2} s^{-1}).

Table 1.

Figure 11:A

Wind velocity = 0 m s^{-1}

(• —— •)	leaf position	1	2	3	4	5
	I	1000	1021	969	761	865
(o- - -o)	leaf position	1	2	3	4	5
	I	1917	1917	2195	1917	1917

Figure 11:B

Wind velocity = 0.2 m s^{-1}

(• —— •)	leaf position	1	2	3	4	5
	I	2813	3000	2990	2750	2750

Wind velocity = 0.6 m s^{-1}

(o- - -o)	leaf position	1	2	3	4	5
	I	2750	2855	2969	2928	2928

Figure 11:C

Wind velocity = 0.4 m s^{-1}

(• —— •)	leaf position	1	2	3	4	5
	I	2105	1948	2532	1948	2000
(o- - -o)	leaf position	1	2	3	4	5
	I	-	2928	2750	2750	-

When a leaf was injured by heat, its temperature decreased very rapidly. The time of this decrease was greatly affected by wind and was also affected by leaf position (table 2). Injury developed earlier and was more pronounced when the upper surface of the leaf was irradiated. An assessment was made of heat sensitivity for the two kinds of leaves. Aspen leaves were injured at a temperature of about + 36°C, while Hibiscus leaves were not injurid until the temperature reached + 44°C. In this discussion, the highest temperature for survival will be called "the critical temperature of the leaf".

Table 2.

Leaf position	1	2	3	4	5
Time of injury (min. after beginning of experiment)	44	108	(none observed)	115	80
Percentage of experiments in which injury occurred	80	30	0	30	40

The results of experiments on water losses from differently positioned leaves are shown in figures 12 and 13, where water loss from the leaves are plotted against time, water loss in this case, being measured as increase in relative humidity in the cuvette containing the leaves. The water lost from the leaves was less when the lower surface of the leaf was irradiated, and smallest when the leaf was placed in position 3. However, two types of curves were obtained (figure 14). At moderate irradiation intensity, a peaked curve (type B) was obtained, but as irradiation intensity increased, the peak flattened out until a plateau-type curve (type A) was obtained. Experiments with leaves placed in position 1, and to a smaller degree leaves placed in position 5, resulted more often in curves of type A than leaves placed in position 2. Experiments with leaves placed in position 3 and 4 never resulted in curves of the A type. When a leaf model, made of wet blotting paper cut into the shape of Hibiscus leaves, was placed in different positions in the cuvette (figure 15), type A curves were obtained.

Since the first part of the curve was the part from which comparisons could be made, regardless of whether the curve was type A or type B, only this first stage was used in comparing results of the different leaf positions.

Whenever type A curves were recorded, the difference in temperature of air entering and leaving the cuvette often resembled the water loss curve of the same leaf (figure 16). The temperature within the cuvette increased about $10^{\circ}C$ in half an hour and about $12^{\circ}C$ in one hour at an irradiation intensity of 1500 joule m^{-2} s^{-1}.

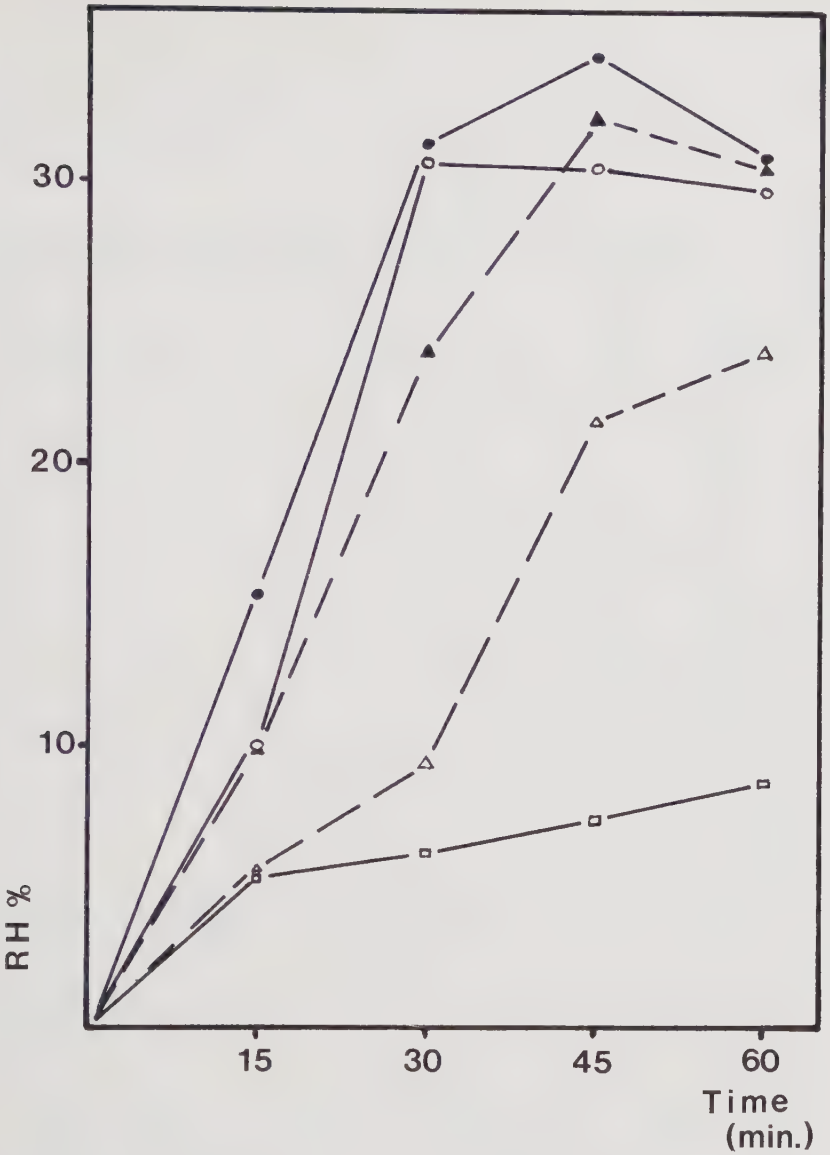
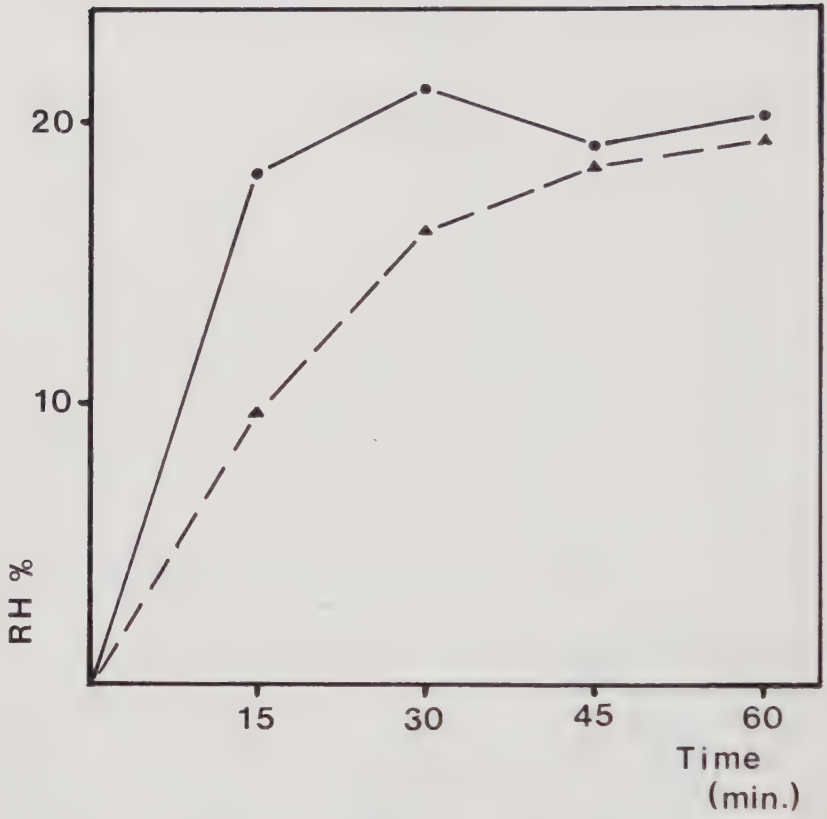


Figure 12. Relative water loss (as indicated by increased relative humidity in the cuvette) from Hibiscus leaves placed in different positions (see figure 2 for description of positions 1 to 5). I = 1500. (● —— ●), (o —— o), (□----□), (▲----▲), (△----△), leaves in position 1 - 5 respectively.


20
10
RH %
15
30
45
60
Time
(min.)

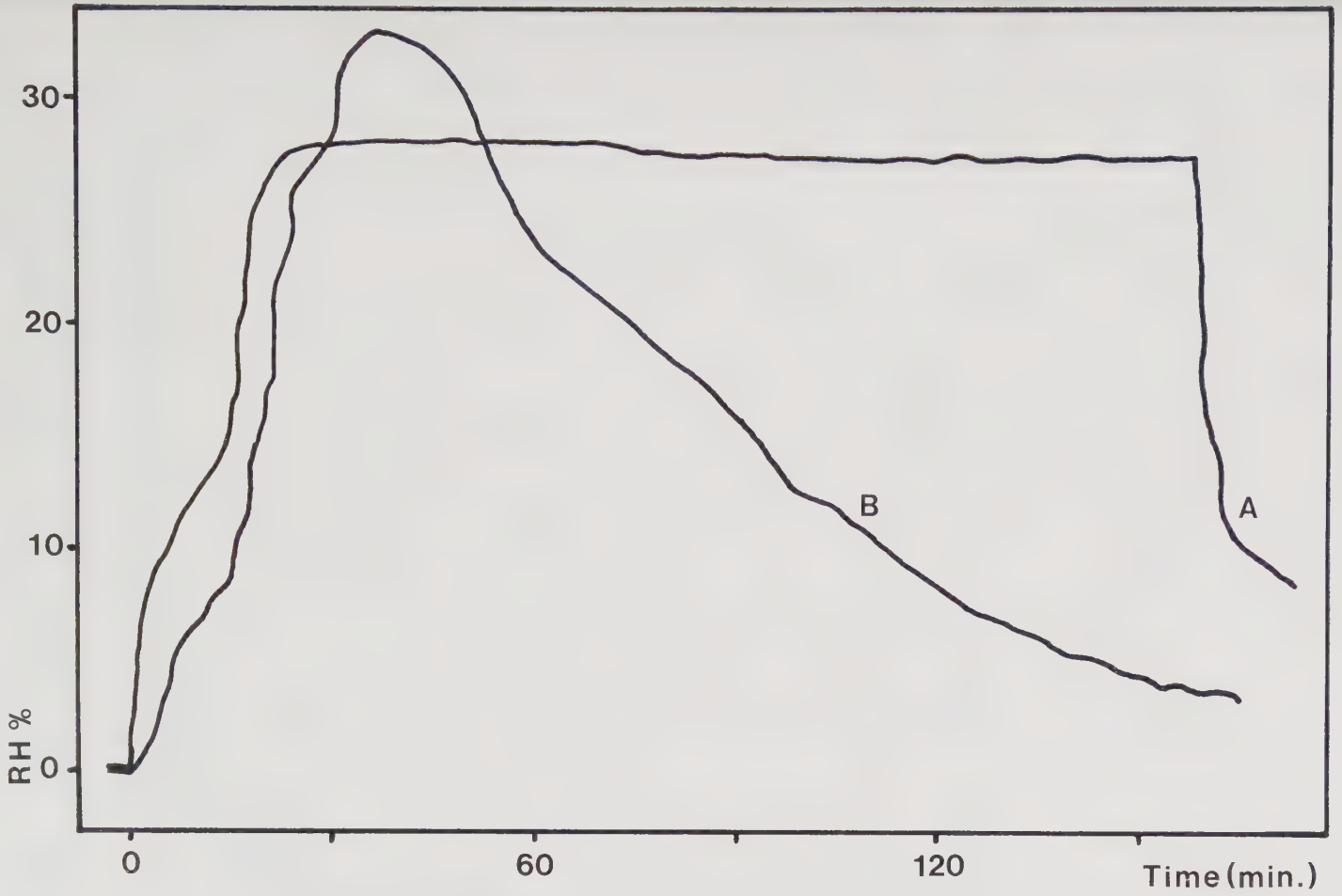
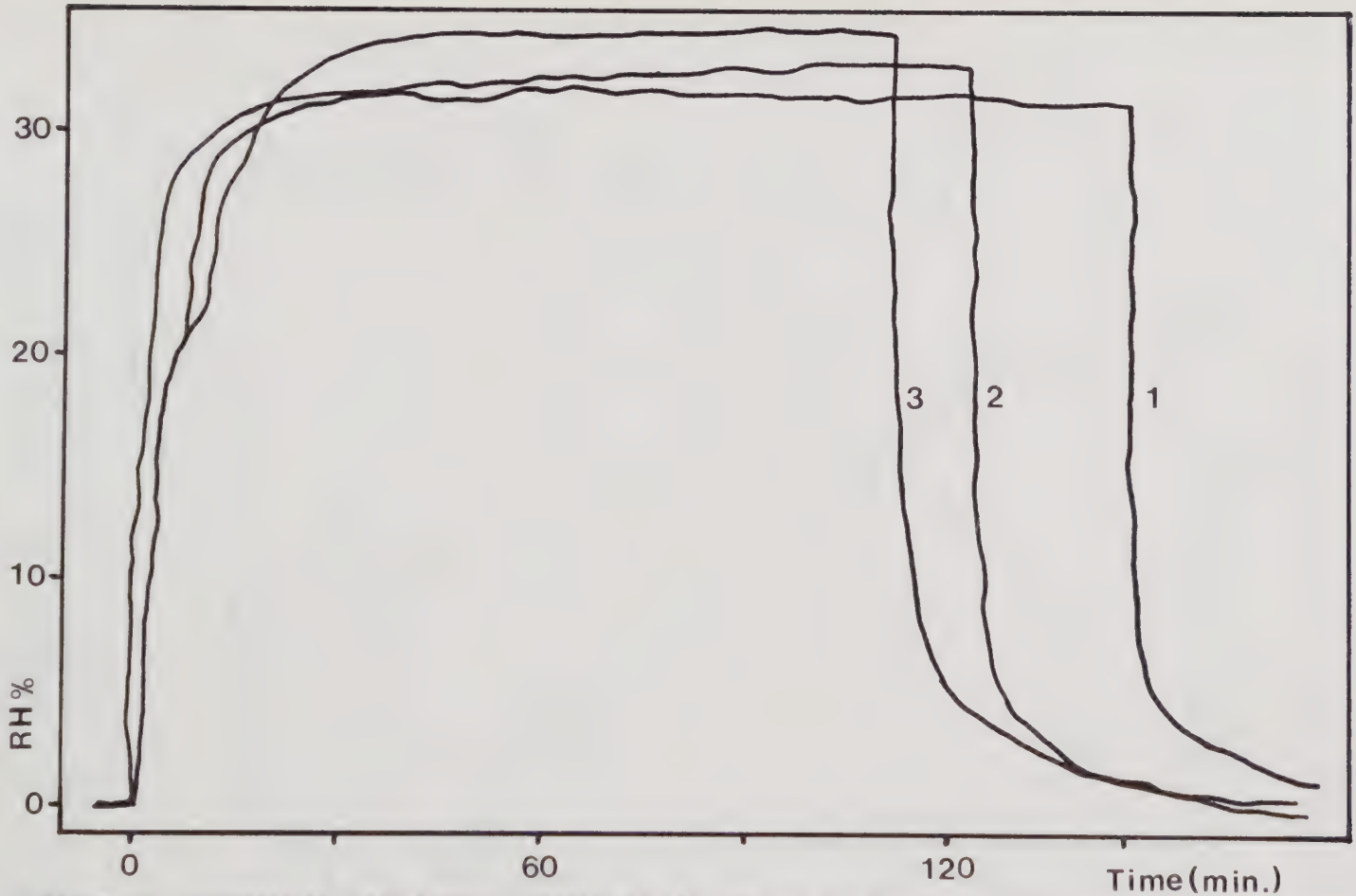


Figure 14. Water loss from Hibiscus leaves placed in position 1. I . 2000.


30
20
10
0
RH %
0
60
120
Time (min.)
3
2
1

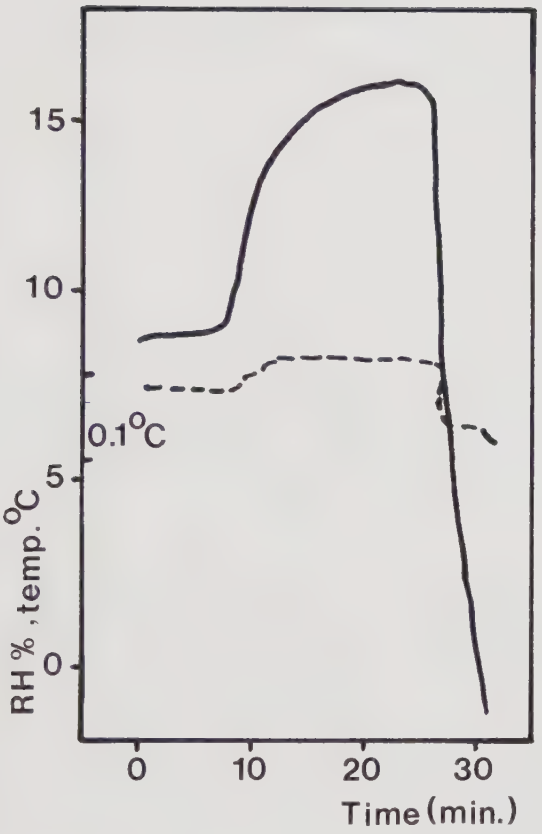


Figure 1. The recorded temperature of the air-stream before and after the passage through the cuvette and the recorded change in water losses from an aspen leaf (A type curve). (———) water losses, (-----) temperature of the air. I 1667.

The result of the determination of stomatal apertures of aspen leaves is shown in figure 17. When the upper surface of the aspen leaf was irradiated, the stomata width was larger than when the lower surface of the leaf was irradiated. At low levels of irradiation (about 700 joule m^{-2} s^{-1}) the stomata of the leaf in position 1 and 5. seemed to close, at higher levels of irradiation they opened. The reverse was true for the leaf in position 2 and 4.

DISCUSSION

The energy balance of a leaf depends on a number of factors; those which cause leaf temperatures to rise can be called "increasing factors", and those which cause leaf temperatures to fall can be called "decreasing factors". The most important increasing factor is direct solar radiation, but longwave (heat) reradiation from the air, the soil, and objects near the plant are also important. These act as radiation partners, since the amount of heat flowing to and from a plant depends on its temperature and that of its surroundings.

Transpiration decreases the temperature of the plant both through evaporation and through its effect on the rate of water flow through the plant. The temperature of the water flowing into a leaf affects its temperature and thus its reradiation balance.

Its reradiation balance is also influenced by the temperature and water content of the boundary layer and of the adjacent air and by the thickness of the boundary layer. The thickness of the boundary layer is determined in part by convection, both free and forced.

When radiation intensity increases the temperature of the leaf increases. Even fairly low energy fluxes have this effect. This temperature increasing effect seems to be linearly related to the increase in radiation intensity. Only at high levels of irradiation intensity, above 2000 joule m^{-2} s^{-1}, is the pattern changed. with a resulting leaf temperature decrease. This result is unexpected, but it is linked to a prolonged survival of the plant. A possible explanation is that increased air movement caused by increased heat absorption in the boundary layer, counteracts the temperature increase of the leaf.

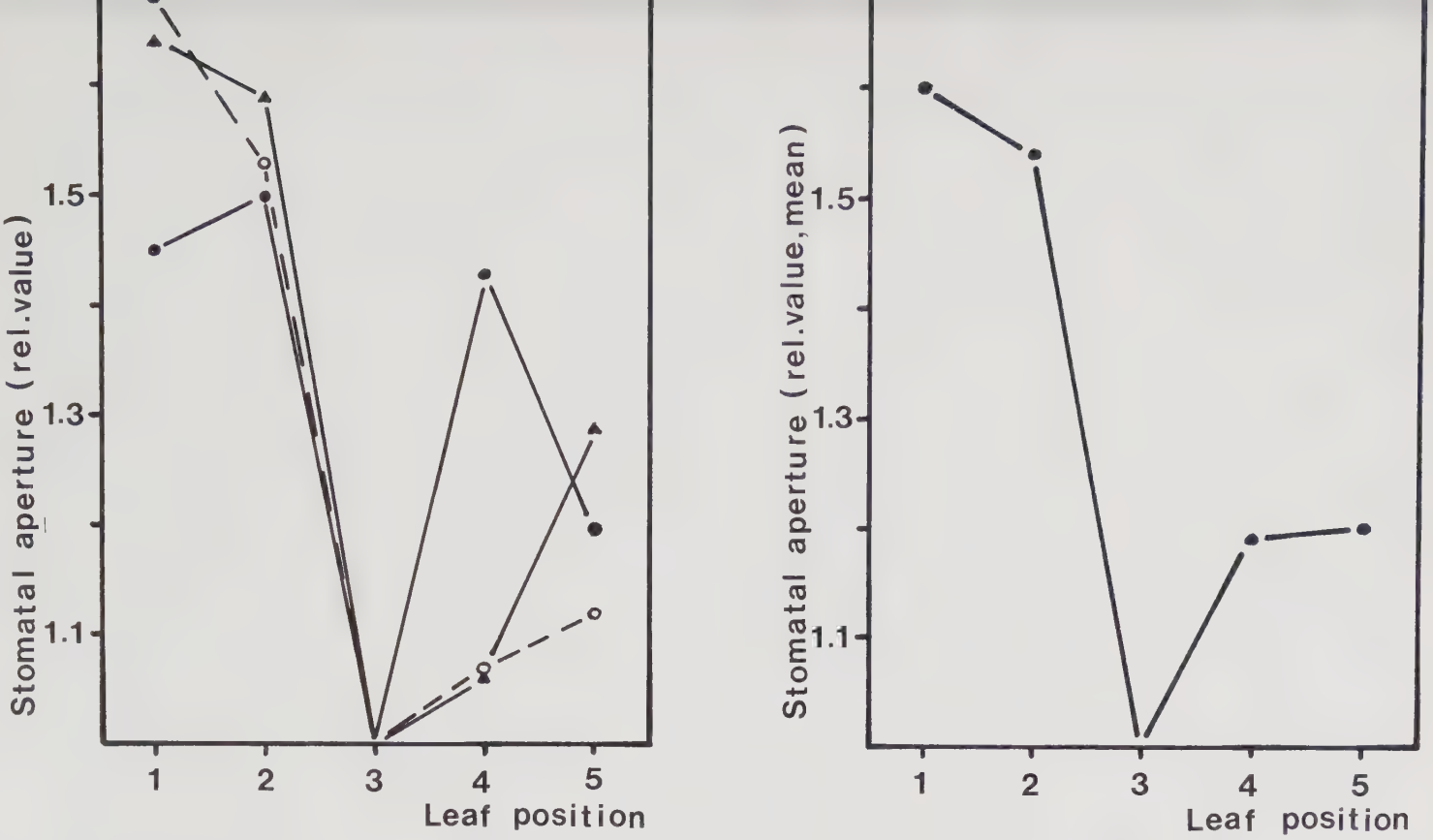


Figure 17. Stomatal aperture of aspen leaves placed in different positions, relative to the stomatal aperture of leaves placed in position 3. Irradiation intensities: (● —— ●), (o----o), (▲——▲); 700, 1167 and 1667 joule m^{-2} s^{-1} respectively.

The fact that the leaf margins have a higher temperature than the central parts is explained by the heat absorbing properties of water in the leaf. During its movement from the petiole through the leaf, the water absorbs heat radiation and is consequently warmer when it reaches the margins. At the edges of the leaf the boundary layer is thinner, which increases heat losses, and thus the outer edges of the leaf are cooler than the margins (2 to 4 mm from the edges).

In this study, the direct radiation of the lamp was much stronger than the direct solar radiation in the field. However, the sum of direct solar radiation and reradiation from the surroundings of a plant gives values near those used here. For example, in June, actual measurements of total heat radiation to a horizontal surface made at Hamburg, Germany, and the estimated values for the same latitude (53°N) in Alaska are equal, amounting to about 1750 joule m^{-2} s^{-1}. Total heat radiation in the alpine tundra of Colorado (40°N) was estimated by Gates (1963) to be about 2580 joule m^{-2} s^{-1}. In this study, the irradiation intensities are typical to values found in the field.

Wind velocities greater than 0.3 m s^{-1} reduced leaf temperatures. When the wind velocity was 0.2 m s^{-1} or slower, the effect on leaf temperature was nearly the same as in still air. The air in the laboratory usually fluctuates between 0.1 and 0.3 m s^{-1} (Raschke 1960) and transpiration alone can cause air movements up to 0.2 m s^{-1} (Gäumann 1942). Increasing wind velocities reduce the thickness of the boundary layer from several cm to about one mm (Berger-Landefeldt 1968, van den Honert 1948, Raschke 1960) and humidity near the leaf is simultaneously reduced. Above 0.4 m s^{-1} it probably causes a change from turbulent to laminar flow around the leaves, besides introducing higher air movements than normally occur in the laboratory. As a consequence, the thermal surroundings of the leaves will be more stable and reradiation to the now lower temperature of the ambient air will increase. The boundary layer of the upper surface of the leaf is thinner than that of the lower surface. The effect of increased wind velocity is consequently greater on the upper surface of the leaf (see figure 10). The temperature of the irradiated upper surface of the leaf is less than that of the lower surface at high wind velocities, which is likely due to the easily reduced boundary layer and the higher reflectivity of the upper surface (Gates and Tantraporn 1952).

Leaf temperature was dramatically influenced by leaf position. The temperature of leaves placed in position 3 was, as a rule, lower than the temperature of the ambient air, and always much lower than the temperature of leaves placed in other positions. In position 3, the area of a leaf exposed to incident radiation is very small and consequently they could absorb only small amounts of radiation. Leaves placed in other positions were always warmer than the adjacent air. The temperature of leaves placed in positions 1 and 5 was always higher than that of leaves in positions 2 and 4. When the lower surface of the leaf was irradiated, its temperature was slightly higher than that of the upper surface. Since the reflectivity of the upper surface of a leaf is greater than that of the lower surface, the temperature of the upper surface is expected to be less than that of the lower surface when both are irradiated at the same intensity level.

Injury to leaves usually appeared at irradiation levels above 2100 joule m^{-2} s^{-1}. With increasing irradiation level the leaf blade was discoloured in a series: light green, yellow, red, and brown. In the major veins at the base of the leaf "plugs" often formed, being discoloured in a similar series. The upper half of the leaf blade showed injury soon after the appearence of these "plugs". The lower part of the leaf blade remained alive in most experiments, probably due to the "conducting capacity of the minor veins" (Wylie 1938). The avoidance of injury caused by heat radiation seems to be coupled with the water transported into and through the leaf blade.

High levels of irradiation (above 2800 joule m^{-2} s^{-1}), generally injured the leaves rapidly. Presumably the increased free convection at the leaf surface set up rapidly superseding eddies which removed the water vapor in the boundary layer that ordinarily absorbs considerable heat. There have also been periodic superseding eddies observed on the lower surface of a Hibiscus leaf (Thofelt 1975 b).

Injury never appeared when the irradiated leaf was placed in position 3, and seldom when the lower surface of the leaf was irradiated (table 2). Since little heat is absorbed by the leaf in position 3, and consequently, the temperature of the leaf is low, it is not injured. The content of water vapor in the boundary layer is one to five per cent higher than in the ambient air (Gäumann 1942). The relative humidity at the lower surface of the leaf is higher than at the upper surface (Yarwood and Hazen 1944). When the lower surface

of the leaf is irradiated, the water vapor of the boundary layer absorbs the heat radiation, acting as a heat filter. The difference in the amount of injury between the irradiated upper and lower surface might be explained by the difference in amount of water vapor available to absorb the heat radiation.

When wind velocities were equal to or greater than 0.6 m s^{-1}, no injury appeared. Little injury was observed when the wind velocity was 0.4 m s^{-1}. Wind velocities of "0" and 0.2 m s^{-1} resulted in the same amount and type of injury. When the wind velocity is higher than 0.4 m s^{-1}, the air movement changes from free to forced convection. When heat transfer through convection increases, less injury occurs. In the light of this, it is puzzling that a wind velocity of 0.1 m s^{-1} resulted in greater injury and shorter survival time than other wind velocities including "0" m s^{-1}. This phenomenon cannot at the present time be explained.

When the critical temperature of aspen and Hibiscus l aves w exceeded, injury appeared. In this study, the critical temperature of aspen leaves seemed to be very low compared to what one would expect in the field. The aspen leaf is apparently capable of avoiding heat stress in the field by its fluttering movement, which increases air turnover, effects reradiation, and increases water flow by means of a pumping action in the petiole (Golovchenko 1974). The critical temperature of aspen leaves in the field, therefore, can be expected to be higher than the critical temperature observed in the laboratory experiments of this study. The difference in critical temperature between the aspen and Hibiscus leaf may depend on genetical differences in their cell membranes. Hansson-Mild (1974) has shown that the water uptake of frog eggs depended upon the temperature, and that two frog species differed in that aspect.

To measure transpiration by existing methods, cuvettes made from various plastic materials are used. Consequently, the radiation balance of a plant is changed through the spectral properties of the cuvette. Trichett and Goulden (1958) showed that some plastics, including "Perspex", a polymetacrylate, were impenetrable by radiation above 7/um, and reduced radiation of wavelengths 4 to 7/um by 50 %. The plastics reflected 6 to 8 % of incoming radiation and were hygroscopic. Even extremely thin water films (2/um) can be the most intensive absorbers of radiation. The water films absorbed effectively at wavelengths of 2.5 to 3.2/um and also at wavelengths above 6/um.

A cuvette made of polymetacrylate is then, a heat-trap. Reflection of longwave radiation emitted from the leaf and from the walls of the cuvette should be measurable. Heat is further accumulated by the water bound to the cuvette walls and by the walls themselves. Heat is lost by conduction through the walls of the cuvette and by reradiation and convection from the outer surface of the walls. Consequently, the thickness and heat conducting properties of the cuvette walls regulate the heat losses. If the cuvette is cooled, these diadvantages are reduced, but not eliminated; the design of the cuvette may also reduce these disadvantages (cf Jarvis and Catsky 1971). The cuvette used in the present study was by no means ideal, being square, rather small, and made of polymetacrylate but it made it possible to get an idea of the influence of radiation on water losses from leaves placed in different leaf positions.

The heat-trap effects on the "chamber-microclimate" resulted in temperature increases in the cuvette during the experiments. When irradiation levels were identical, the differences in water lost from leaves placed in different positions must be due to the different leaf positions to incident radiation rather than to "chamber-microclimate" since all leaves were exposed to the same experimental conditions.

The measurement of water losses from leaves in different leaf positions resulted in two types of curves, one a peaked curve and the other a plateau-type curve, as mentioned earlier (figure 14). The decrease following the peak in curve B was probably caused by stomatal closure resulting from a water deficiency in the leaf. In experiments with high irradiation, such a decrease never appeared and water losses from the leaf remained at a high level until a sudden drop showed that the leaf had been killed (curve A). This pattern is similar to that obtained when evaporation from a blotting paper is plotted and it may be assumed that for some reason the stomata did not close. Brunner and Eller (1974) found that the stomata of Piper beetle opened at high temperatures (+ 45°C) in the dark. There might be a similar reason for the transpiration pattern at high irradiation intensities observed in aspen when accompanied by high temperature.

The laboratory experiments with wet paper models were performed in order to get an idea of the influence of changes in air velocity. However, when the direction of irradiation was parallel to the surface

of the paper (leaf position 3), it lost more water than when the radiation was at 45° or 90° to the surface (leaf positions 2 and 1). This result was unexpected. It may be explained either as a wind effect, or as an effect of radiation absorption in the water vapor of the boundary layer. When the leaf model was placed in leaf position 3, the air stream flowed along the two surfaces of the model. The water was thus effectively transported away, compared to the slower transports of water when placed in positions 1 and 2.

Radiation is absorbed in the water vapor of the boundary layer of the model or leaf as well as in the paper itself or in the leaf tissues. The absorption of radiation in the water vapor of the boundary layer is probably more effective in leaf positions 1 and 5, than leaf position 3. This could be due to the greater volume of water vapor exposed to radiation and the slower transport of water vapor from the surface of the model or leaf.

In experiments with living leaves, the results were different from those obtained with wet paper models. This may be explained by a new factor, the stomatal aperture. The water lost from leaves placed in leaf positions 1 and 2 was highest and from leaves placed in position 3 unquestionable lowest. The leaf placed in position 4 lost more water than the leaf placed in position 5, which may be explained by the absorption of radiation in the water vapor of the boundary layer. The leaf placed in leaf position 4 had, as a rule, a lower leaf temperature but higher transpiration rate than the leaf placed in position 5. This is presumably caused by greater heat absorption in the boundary layer, which is thereby reduced. Transpiration is consequently increased.

Obviously the position of the leaf influences transpiration rates.

The results of this investigation suggested that water is the main heat absorbing medium both inside and outside the leaf. The fact that the leaf temperature rapidly falls when a leaf dies adds support to this proposition. When no water is left, transpiration, of course, ceases. One might expect a rise in temperature to follow; however, the energy supply from irradiation is a necessity for the maintainence of a high leaf temperature, and when this supply ceases as a consequence of no absorber being present any longer, reradiation causes a rapid temperature drop.

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II.

THERMOGRAPHIC MEASUREMENTS OF LEAF TEMPERATURE.

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ABSTRACT

Aspen (Populus tremula), birch (Betula verrucosa) and Hibiscus (Hibiscus sinensis) leaves and a Thermovision 680 (102 B equipment AGA AB, Sweden) were used.

The reflectivity of the upper surface was greater than that of the lower. When the lower surface of the leaf was indicated at high intensities, fewer injuries resulted. This could be due to heat absorption of the water vapor of the boundary layer. The temperature is higher at the edges of the leaf and lower at the base, thus the water seems to be the absorber and translocator of heat in the leaf.

Temperature sensors, attached to or inserted into the leaf, results in too high, and too low temperature.

Wounding the leaf results in low temperature, and slower temperature response in the wound. The minor veins increase their transport capacity, reestablishing about the same temperature pattern in the leaf as before the wounding, except in the cool wound.

Thermography is an excellent method of measurement concerning the relative temperature of the leaf and gives a complete picture of the thermal pattern of the leaf. Rapid changes in leaf temperature can be observed and recorded. The results depend on a reference temperature source; the ambient air or a blackbody radiator is suggested.

INTRODUCTION

Leaf temperature is normally measured with some type of temperature sensor attached to the surface of the leaf or inserted into the leaf tissue. The insufficiencies of these techniques for ecophysiological reasons are that the leaf must be held in a fixed position in order to keep the temperature sensor in place, and a wound in the leaf tissue presumably changes the biochemical and heat transfer processes of the leaf. For practical reasons, few temperature sensors can be used simultaneously; this limits the number of measurements which can be taken, making it very difficult to get a total picture of the temperature pattern of a whole plant or even a single leaf. The temperature response of a plant to sudden temperature changes in the micro-climate, e.g. sudden gusts of wind, changing clouds with intermittent flashes of sunshine and/or showers of rain, cannot be adequately followed by methods of measurement based on temperature sensors. The heat transfer between the leaf and its surroundings is more or less altered because of the attaching or inserting of temperature sensors which affect the physiological and biochemical processes in the plant.

These insufficiencies can be overcome by thermographic measurement of heat emitted from an object (Perrier 1971). Rapid temperature changes in the leaf blade or the plant can be registered and afterwards studied in minute detail. Thus, a very exact knowledge of the relative temperature pattern of a leaf can be obtained. In determining the true temperature levels, a reference temperature source must be used. A solution to the problem of choosing a reference source is discussed in the following text.

MATERIAL AND METHODS

Leaves of aspen (Populus tremula), birch (Betula verrucosa) and, in one experiment, Hibiscus (Hibiscus sinensis) were collected from small trees outdoors and, in the case of Hibiscus, from a potted plant. The petioles were cut under distilled water, placed in small test tubes, and left in the dark for at least one hour before experimentation (Thofelt 1975 a). The test tubes were placed in heat insulating plastic foam ("Frigolite") during the experiments.

The leaves were placed with either the upper or lower surface exposed to irradiation (leaf position 1 and 5 respectively, Thofelt 1975 a). An incandescent lamp ("Attralux, Type 13011, Philips, Holland) was used as the energy source. Its colour temperature was 2700 K, and thus supplied a large amount of heat radiation (cf Thofelt 1975 a).

Leaf temperature was measured by a system Thermovision 680/102 B (AGA AB, Sweden), here abbreviated to THV 680, consisting of two separate units: Infrared Camera and Thermal Picture Display, and functioning as a closed-circuit television system. The camera unit converts infrared radiation given off by an object into equivalent electronic signals which are amplified and transferred via an interconnecting cable to the display unit. It had an infrared lens made of silicone with f = 1.8 and a field of view of 10^{o} x 10^{o}, range of focus from 0.95 to infinity, and depth of field of 0.27 m at 2.5 m. The detector consisted of indium antimonide (InSb) photovoltaic with a spectral range of 2 - 5.6 µm. The detector is most sensitive at low temperatures and is therefore cooled by liquid nitrogen in a connecting Dewar flask at a temperature of $-196^{o}C$. The picture size of the TV-monitor picture tube is 90 x 90 mm for direct viewing and 67 x 74 for photographic recording. Picture frequency is 16 frames per second (25 frames per second for the THV 750 which was used for one measurement of the Hibiscus leaf) and there are 210 interlacing raster lines per frame which allows detailed study of the thermal picture.

For temperature measurement, the lens was set at f = 1.8. It was possible to measure temperatures from -30^{o} to $+190^{o}C$ at 10 different sensitivity levels, the most sensitive of which gave detectable temperature differences of less than $0.2^{o}C$ at $+30^{o}C$ object temperature. The isothermic functions could be either dual or single and were variable from 2 to 60 % of the selected temperature range, with levels adjustable continously and independently.

The true temperature of the object must be calculated from the temperature difference between a known-temperature source, which in this study was the temperature of the ambient air, and the object. The isotherm-unit readings were converted to true temperatures with the help of calibration charts. A mercury laboratory thermometer was used to measure the temperature of the ambient air. These temperatures were compared with the readings of the THV 680, and the reflectivity of the leaves was measured when directly and indirectly irradiated.

Infrared radiation from an object consists of reflected and emitted radiation with the reflected portion consisting of specular and diffuse factors (cf Bäckström and Welander 1953, Gates and Tantraporn 1952, Gates et al 1965, Wong and Blevin 1967). Although practically no infrared radiation is transmitted through the leaves (Gates and Tantraporn 1952), it is necessary to measure the proportion between the specular and diffuse factors in order to calculate the temperature of the object.

The leaves were placed in a box 0.8 x 0.6 x 1.1 m made of white cardboard and open on one side. An incandescent lamp was placed in the box pointing towards its ceiling to provide indirect irradiation for one series of experiments, or pointing toward the leaves from a position in front of the open side of the box to provide both direct and indirect irradiation for the other series of experiments. The irradiation level in either case was 183 joule m^{-2} s^{-1}.

The mercury laboratory thermometer was placed in the box and irradiated indirectly and directly. When the lower part of the thermometer was painted black the difference between the temperature readings of the thermometer and of the THV 680 was between 1.5 and 2.5°C. When not painted, the difference between the readings of the thermometer and of the THV 680 was 0.6 to 1.4°C when indirectly irradiated, and 0.2 to 0.5°C when directly irradiated, or about 1°C. The temperature readings of the thermometer were always lower than the temperature readings of the THV 680.

RESULTS

When touching the leaf with a probe or other tool, no effects were observed other than those caused by shading, i.e. leaf temperature lowering.

The reflectivity and transmissivity of the Hibiscus leaf was measured with a THV 750, which has about the same measuring characteristics as the THV 680. No THV 680 was available at the time of measurement. The leaf was placed in test tubes and irradiated at 52 joule m^{-2} s^{-1} on the upper surface and 33 joule $m^{-2}s^{-1}$ on the lower. The camera was placed near the lamp and the lamp was rapidly and repeatedly shaded (about 1 second each way). It was necessary to use low

intensities of irradiation, because periodic superseding eddies appeared at higher levels of irradiation (about 1500 joule m^{-2} s^{-1}).

The infrared "signals" from the leaf were compared when the leaf was shaded and when it was irradiated. In both cases the true temperature of the leaf (as measured with the repeated touch method) was the same. The difference between the two temperature readings of the THV give the approximate reflection of the leaf. The "radiation signal" to the IR-camera is the sum of emitted and reflected radiation of the leaf. The "shaded signal" to the THV is the emitted radiation.

The reflectivity of the aspen and birch leaves was determined from the quotient between the true temperature of the leaf, recorded by the repeated touch method (cf Thofelt 1975 a), and the thermographic temperature of the leaf recorded by the THV 680. The results are summarized in table 1.

Table 1. The quotient between the temperature of aspen and birch leaves recorded by the repeated-touch method and the THV 680.

	Aspen		Birch	
	Upper surface	Lower surface	Upper surface	Lower surface
Indirect radiation	0.97	0.98	0.94	0.95
Direct radiation	0.95	0.96	0.90	0.93

The mean reflectivity of the upper and lower surface of the aspen leaf was 4 % and 3 %, and of the birch leaf 8 % and 6 % respectively.

The reflectivity of the upper and lower surface of the Hibiscus leaf was found to be 10 $\pm$ 1.5 %, and 11.5 $\pm$ 1 % respectively, which includes the source of error made by the operator when reading and interpreting the signals.

The transmission of light through leaves was investigated as follows: a leaf was placed near a hole (40 mm diameter) in a 1 cm thick board with the lamp on the same side of the hole as the leaf and with the camera on the opposite side. The leaf was rapidly and repeatedly shaded (about one second each way) and the temperature signal was read as in the other experiments. Incident radiation was 33 joule m^{-2} s^{-1}. There was no indication of transmission through the Hibiscus leaf so transmission was assumed to be zero (cf Gates and Tantraporn 1952).

In the figures, or thermograms, here abbreviated tg 1 to tg 5, the results of these experiments on the heat relationship of the upper and lower surface of leaves, the effects of temperature sensing devices on leaf temperature, and the effect of wounding on leaf temperature are summarized. Because we could not detect any differences in reflection at different wavelengths of radiation with our equipment we assumed reflectivity to be five per cent and transmissivity to be zero (Wong and Blevin 1967).

Experiment 1. Comparison of the upper and lower surface of the aspen leaf and the maximum temperature response to irradiation. Two replications of this experiment were conducted: thermograms 1:1 to 1:25 summarize the results of one replicate (Experiment 1 A), and thermograms 2:10 to 2:45 the results of the other (Experiment 1 B). The number following the colon in each of the thermograms indicate the number of minutes since the experiment began.

Experiment 1 A. The upper and lower surfaces of aspen leaves were irradiated with the same incandescent lamp (tg 1). It was impossible to get exactly the same irradiation level to both leaves; irradiation levels were 2100 joule m^{-2} s^{-1} to the left leaf (leaf position 1) and 2300 to the right leaf (leaf position 5).

The leaf with the lower surface exposed to irradiation reached its highest temperature, +44.7°C after 25 minutes, and had a mean maximum temperature of 42.6°C. The leaf with its upper surface exposed to irradiation reached its highest temperature in one minute, +46.5°C, and had a mean maximum temperature of +44.7°C.

When the incandescent lamp was turned off, the temperature dropped 18.6°C in one minute, and 24.6°C in two minutes, from +44.7°C to 26.1°C and 20.1°C respectively. When not irradiated, both leaves had the same temperature.

The termograms show the temperature distribution over the leaf blade for both leaves. The temperature rose more rapidly in the leaf to the left, which is indicated by the greater white area. The last thermogram in the series demonstrates the effect of leaf position on leaf temperature. The cool area in the centre of the leaf, as indicated by the gray-tones of the thermogram, was greater in the leaf with its lower surface exposed to irradiation than the leaf with its upper surface exposed. In both leaves the lowest temperatures were found near the leaf base and near the edges of the leaf. After about

20 minutes, injuries appeared in the upper half of the leaf blade of both leaves. Injury was more severe in the leaf placed in position 1.

The uneven temperature distribution in the thermograms indicate rapid fluctuating temperatures of the leaf blade. These were readily observed on the TV monitor screen but it was not possible to document this with the equipment available.

Experiment 1 B. Irradiation levels were 2550 and 2700 joule m^{-2} s^{-1} to the leaf placed in positions 1 and 5, respectively. These irradiation levels are high and heat injuries developed rapidly (tg 2).

During the first ten minutes there were great temperature fluctuations on the surface of the leaf that had its lower surface exposed to irradiation. These fluctuations looked like flames. After ten minutes the isotherm covered the maximum area of the leaf blade. After twenty minutes, injury covered 75 % of the leaf blade in position 1 and 45 % of the blade in position 5. The area of injury corresponded to the isotherm marking the maximum temperature in the leaves.

The injuries that developed during the experiment were correlated with the temperature patterns of the leaves, as marked with the isotherms (tg 2:30,35). The leaf temperature dropped as the leaves dried. The highest leaf temperatures were found near the base of the leaf, except the area near the petiole. The veins of the leaf were cool compared to the leaf blade (note the gray-tones in tg 2).

The leaves first began to visibly dry; this was followed by an accentuated rise in temperature followed, in turn, by a temperature drop to a lower level where it stabilized (tg 2:35). The temperature in the centre of the leaf again rose. At the end of the experiment, the centre of the leaf was soft but uninjured. The rest of the leaf blade, except the base of the leaf, was dry (tg 2: 40,45).

The isotherm of the last thermogram in the series shows a difference in temperature between the leaves in the two leaf positions (tg 2:45). The isotherm covered a greater area of the leaf blade placed in position 5, but only covered the bigger veins near the base of the leaf placed in position 1. The leaf placed in position 1 was markedly more injured, and dry, than the leaf placed in position 5.

Experiment 2. The effect of temperature sensors on leaf temperature, attached to or inserted in an aspen leaf. An extension tube was attached to the IR-camera.

Experiment 2 A. A simulated temperature sensor attached to the lower surface of a leaf (tg 3).

This method of measurement corresponds to methods used by other workers (see Thofelt 1975 a, Perrier 1971). A small soldered ball (diameter 3 mm) attached to two naked, bright wires (diameter 3 mm) was fastened with black adhesive tape, about 3 x 3 mm square, to the lower surface of the leaf. The lower surface of the leaf was irradiated (leaf position 5). The first thermogram shows the position of the simulated temperature sensor (tg 3:2). The warmest part of the leaf was the right upper part seen from the IR-camera. It is also evident that the parts around the tape and the "temperature-sensor" were warmer than the leaf blade. The part covered by the tape was still warmer as is seen by the very light gray-tones of the thermogram. After nine minutes, the leaf was turned to position 1 and the upper surface of the leaf was irradiated. The highest temperature of the leaf was found in the left, upper part of the leaf blade exactly where the "temperature-sensor" was placed. A rapidly disappearing warm spot was found near the petiole (tg 3:9). The temperature distribution of the leaf during the latter part of the experiment was as shown in tg 3:14. Experiments with transparent tape gave similar results.

Experiment 2 B. A simulated temperature sensor inserted in the leaf mesophyll.

This method of leaf temperature measurement is commonly used (Thofelt 1975 a).

The simulated temperature sensor (a thin bright wire 4 x 0.3 mm) was inserted into the leaf mesophyll near the epidermis on the lower surface of the leaf. It was placed parallel to and near the central, longitudinal vein. The lower surface of the leaf was irradiated (leaf position 5). At first the temperature of the wound dropped, except where the temperature sensor was inserted into the leaf mesophyll. The temperature was lowest in the wounded mesophyll and higher at the point of insertion (cf tg 4:2). The gray-tones of the thermogram indicate that the temperature of the wound was even lower than the temperature of the edges of the leaf. The temperature of the wound leaf blade gradually rose (tg 4:4,8,10).

After turning the leaf to position 1, the same temperature distribution was observed. The wound had the lowest temperature of the leaf blade, except at the point of insertion. Injury appeared in the centre of the leaf after about twelve minutes. Two minutes later, the leaf

blade was warmer with an even temperature, except at the cooler edges of the leaf. The warmest parts of the leaf were the outer parts and the wound (cf tg 4:14).

Experiment 3. Temperature changes caused by wounding an aspen leaf.

The effects on leaf temperature when wounding the leaf were studied as follows: the lower surface of a leaf was scratched straight across at right angles to the central vein. The operation resulted in very rapid changes in leaf temperature all over the leaf blade. The most dramatic temperature change appeared in the wound (cf tg 5) where the temperature dropped rapidly and distinctly. The leaf blade distal to the wound grew cooler (darker gray-tones) than the rest of the leaf blade. The temperature of the leaf below the wound dropped slightly during the experiment. Low temperatures were found near the petiole. The veins of the leaf had higher temperatures than the leaf mesophyll. It was especially evident in the distal parts of the leaf mesophyll. After about ten minutes, the leaf temperature returned to almost the same condition as at the beginning of the experiment.

DISCUSSION

The experiments illustrate the role of water in the leaf as an absorber and translocator of heat (Thofelt 1975 a). When one point of the leaf is heated, as in experiment 2 A, the water in the leaf is heated at that point and transported toward the edges of the leaf (tg 3:2,9,14). The base near the petiole, and the edges, were the coolest parts of the leaf blade. The maximum temperature of the leaf was found in the outer parts of the blade (tg 4). The water consequently absorbs heat during passage through the leaf.

When the leaf dried (cf also Thofelt 1975 a), the temperature of the leaf decreased rapidly. This must be caused by reradiation since transpiration ceased when the leaf was killed. Of these two processes, reradiation then (with maximum at 8.9 and 10 μm according to Raschke 1960) must be the most important heat losing process.

Near the edges of the leaf, the boundary layer is small. Heat losses are here effective due to the small distance of transport in

this thin boundary layer. Consequently, the edges of the leaf have a low temperature.

The water flowing in the leaf absorbs heat radiation. In tg 5:2 the upper part of the leaf becomes cooler which is caused by the impeded water transport in the scratch. The veins remain warmer than the mesophyllic parts. The cooling effect of transpiration affects the veins later because more water is kept in the veins than the mesophyllic parts. After about ten minutes in the experiment, the temperature distribution of the leaf returned to the original, un-wounded state. The results may be compared to the observations of Wylie (1938) concerning the water transports of the minor veins of foliage leaves. Even if many veins are severed, as in this experiment, the remaining functioning veins increase their water transports and thus maintain about the same temperature conditions of the leaf as before.

Water vapor outside a leaf acts as a heat filter. If we assume that heat is mainly absorbed by water, we can understand why the leaf temperature becomes higher when the leaf is irradiated from the upper surface than from the lower. The lower surface is protected from the irradiation by water vapor given off from the stomata. According to Fowle (1917), cited by Curtis (1936), water vapor has strong absorption bands in much the same region of infrared as liquid water. Water films absorb heat radiation very effectively (Trichett and Goulden 1958) as does water (Gates 1963, Hoffer and Johanssen 1969). Liquid water effectively closes the atmospheric window (Lowry 1972).

The tape and the temperature sensor absorbed heat in the experiment involving them and the scratched leaf. Only the tape was warm, the wounds were cool. Changes in the physiological processes of the leaf must have occurred in the wound.

When a leaf was wounded, the temperature response of the wounded area was found to be different, usually slower, than the response of the unwounded parts of the leaf blade. It was also found that when the experiment of wounding the leaf was repeated in early autumn (or about one month later), the temperature response of the leaf was much slower. However, the wounded area was cooler than the unwounded parts of the leaf blade.

The reflectivity of the birch leaf seems to be higher than that of the aspen leaf in the wavelength band used. The reflectivity of the Hibiscus leaf is higher than that of the aspen and birch leaf. The upper surface of the aspen and birch leaf reflects more than the lower

surface (cf Gates and Tantraporn 1952). The specular reflectivity of the birch and aspen leaf seems to be larger than the diffuse, as found in these preliminary experiments. The reflectivity was about 5 % for the birch and aspen leaf, and about 10 % for the Hibiscus leaf, in wavelengths measured with the THV 680 equipment. The reflectivity of leaves is higher at about 1 /um (Hoffer and Johanssen 1969, Wong and Blevin 1967) and about 65 % for the birch and aspen leaf at about 0.8 /um with slight seasonal differences (Bäckström and Welander 1953).

Increased air movements near the leaf surface (Thofelt 1975 a) were observed in an experiment with Hibiscus leaves, and appeared as periodic superseding eddies. In an experiment with aspen leaves, these were not observed. It is possible that the periodic superseding eddies owe their origin to the interaction between irradiation, presumably also wind, and the structure, shape, and area of the investigated leaf. The periodic superseding eddies are "bubbles of superheated air", growing in size", and rising from the surface (Lowry 1972), and in that way transporting heat (and water) from the surface of the leaf. When such a bubble leaves the leaf surface, the boundary layer may be destroyed. Heat radiation and hot air near the surface of the leaf can then work with full effect on this water vapor unprotected leaf surface, and injury (burns) may develop (cf Gates 1963). The Hibiscus leaf has the structure and form necessary for the origin of these superseding eddies, the aspen leaf does not.

Remote sensing methods are preferable to other methods of leaf temperature measurements because these methods do not interfere with the normal energy budget of the plant. THV 680 provides an excellent method of measurement because the system works far from the plant, measuring true and relative temperature. Rapid temperature changes can be observed and recorded and different parts of the object can be later compared. Also, thermal influences of the surroundings can be evaluated (cf Thofelt 1975 c). However, the specular and diffusive reflection of infrared radiation from the plant complicates the measuring of the true temperatures of the object by these remote sensing methods. It is thus necessary to use for reference an object of known temperature. The temperature of the ambient air is a very convenient reference temperature source, but is not easy to measure adequately because the reference object must be within the thermal picture and consequently must have small dimensions, yet must be big

enough to enable temperature measurement by thermography. The known temperature source should give an adequate estimate of the radiation regime and the influence of free and forced convection. For that purpose, it would be possible to use a hollow metal sphere mounted on a handle, painted dull black outside and inside, with thermocouples mounted in different positions inside the sphere. Such a black-body radiator could be mounted near the object and used as a reliable reference temperature source because it would have the same temperaturse as that of the ambient air. Or a simulator of black-body radiation in the temperature interval of -5° to about $+60^{\circ}$C with individually calibrated steps of 1°C could be useful. Calibrated variable temperature sources are commercially available today (AGA AB, Sweden), but these are too big and disturb the energy turnover of the leaf, as was found in some experiments. A small temperature reference source (about 10-15 mm in diameter) mounted on a long movable arm should eliminate this difficulty. Nevertheless, the temperature of the ambient air with some type of black-body radiator is superior.

THV 680 provides a rapid method for leaf temperature measurement with the capability of choosing isotherm levels and sensitivity levels according to the temperature conditions of the object. However, the system of documentation must be adequately chosen. The video-tape recorder is preferable when temperature changes of the object are rapid and frequent. The C-12 camera ("Tektronix") can be used for most experimental purposes. Documentation with the C-12 camera is a rather slow method because making the thermogram takes some time and the camera works at 1/5 second. The thermogram is consequently a sort of mean value of the recorded temperature pattern of the object.

Cine cameras and 35 mm cameras are not recommended. It is necessary to control the quality of the thermogram immediately, and this is not possible with regular cameras.

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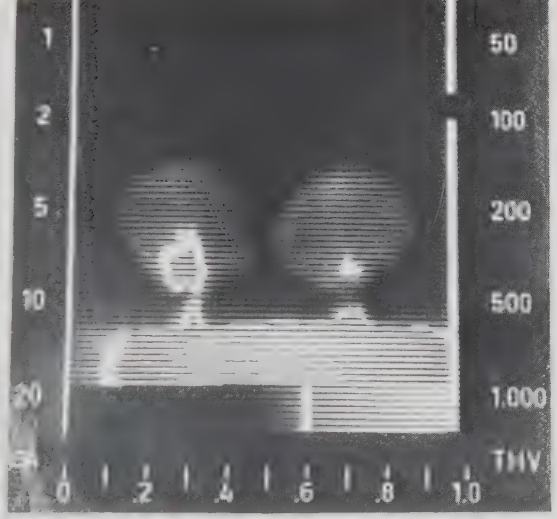
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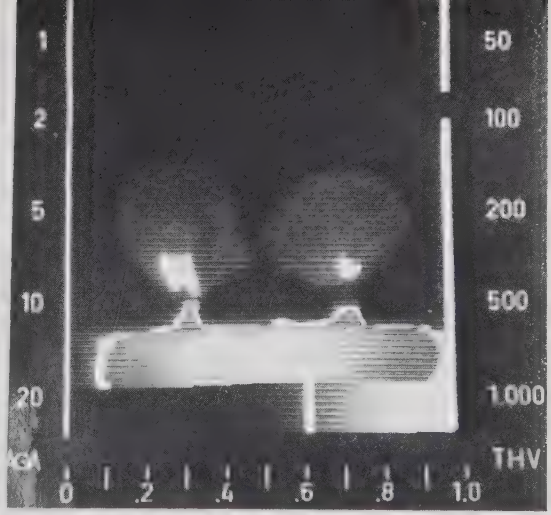
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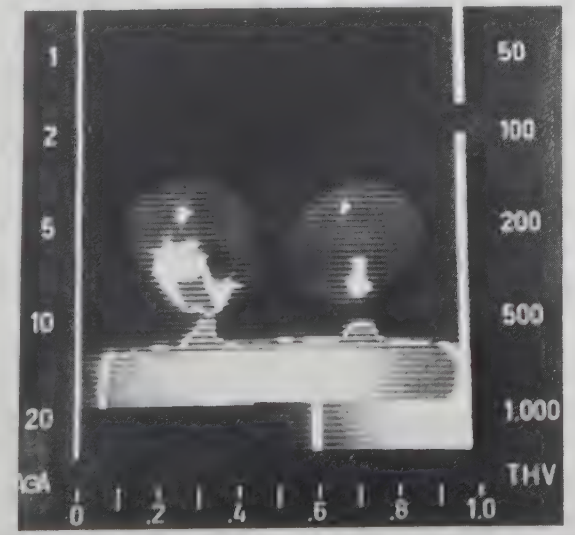
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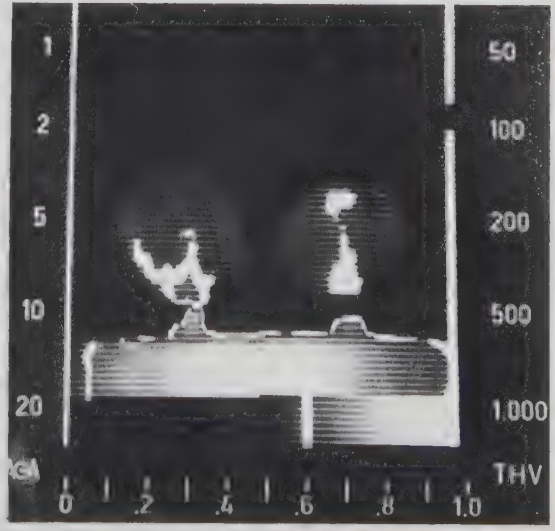
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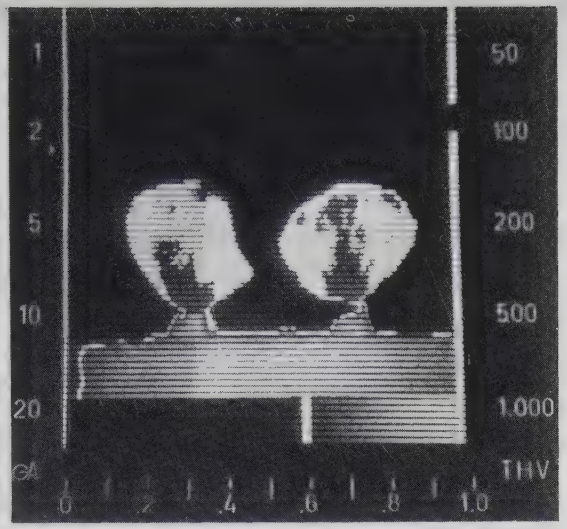
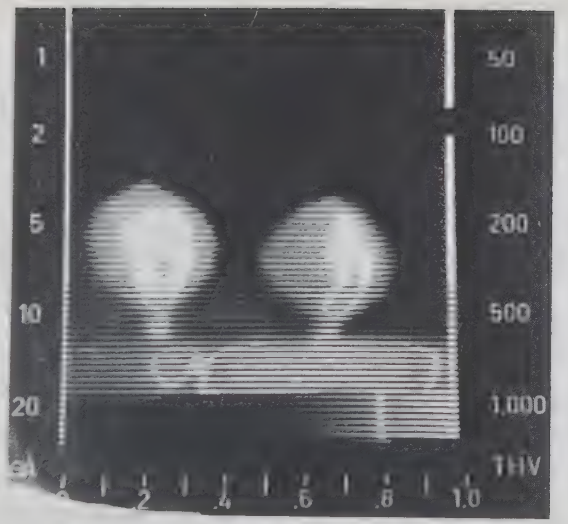


tg 1:15

tg 1. The difference in temperature between the upper and lower side of aspen leaves when irradiated. The left and right leaf is placed in leaf position 1 and 5, and irradiation with 2100 and 2300 joule m^{-2} s^{-1} respectively. tg 1: 1, 2, 4 etc. is the experiment number followed by minutes from the start of the experiment. The isotherm width (or selected temperature range) at the isotherm level 0.6 (the marking of the "abscissa" of the thermogram) gives the temperature range at about 40.5 - 41.8°C. All areas with this temperature is marked in white. The gray-tones of the thermogram indicate higher temperatures when lighter, lower temperatures when darker. It is not possible to determine true temperature levels with the gray-tone scale. Cf text.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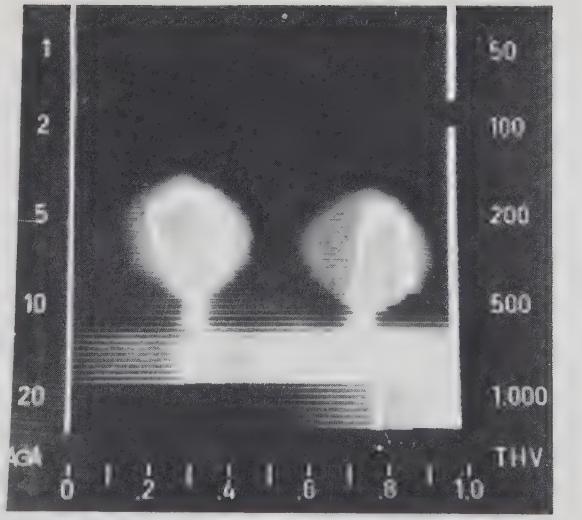
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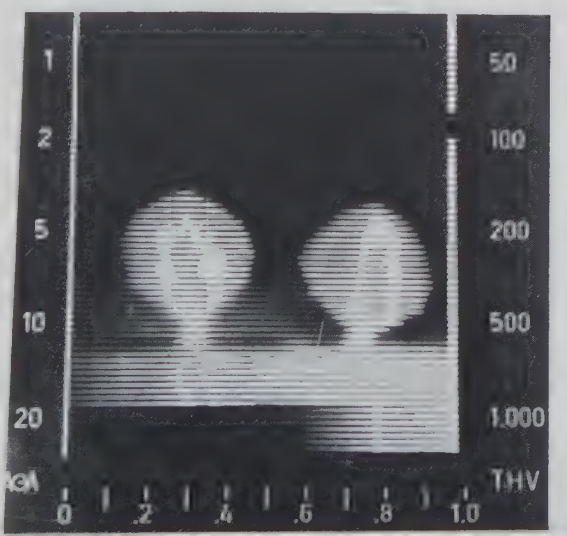
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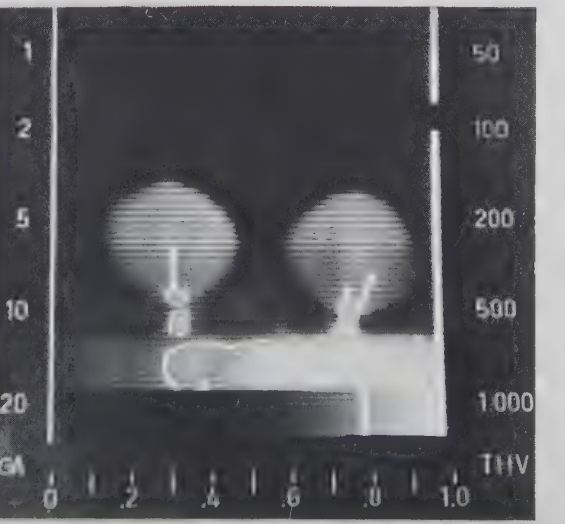
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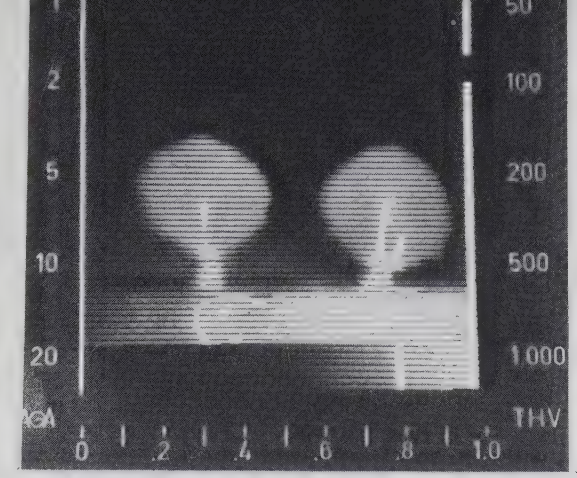

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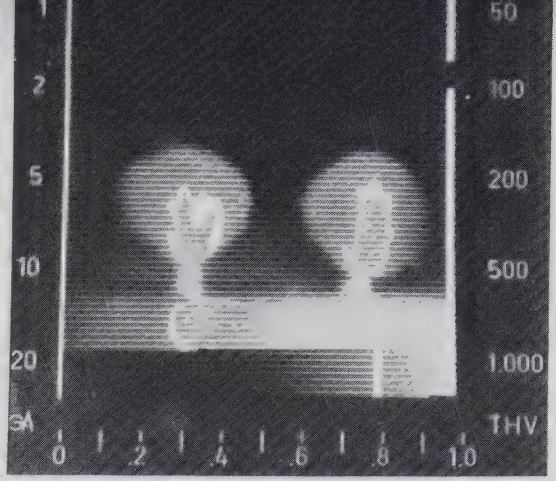

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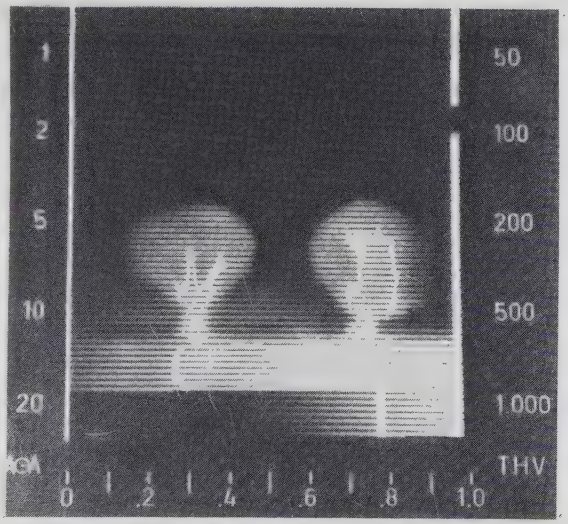
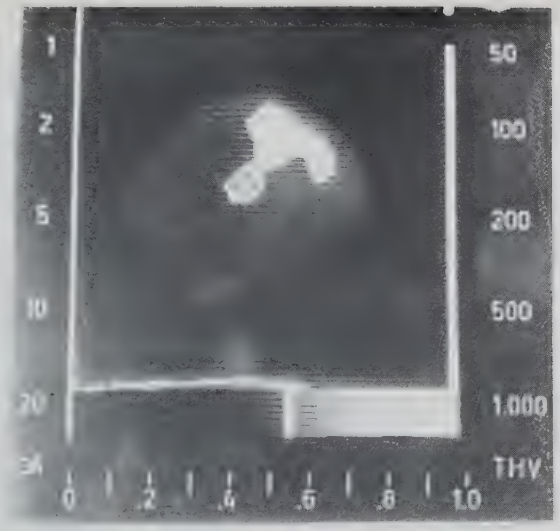
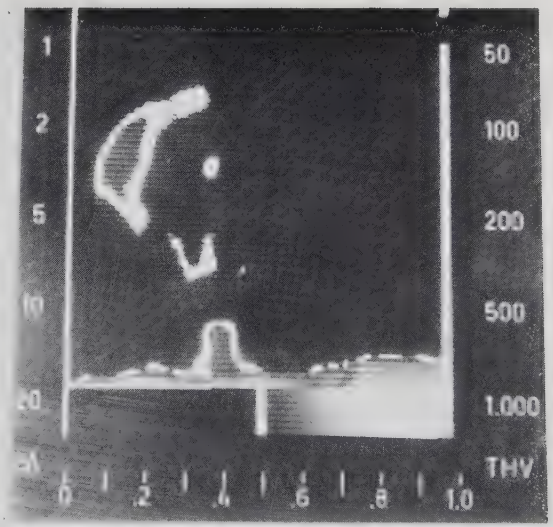


tg 2:45

tg 2. The effect of high irradiation on leaves placed in leaf position 1 and 5. The left and right leaf is placed in leaf position 1 and 5, and irradiated with 2990 and 7200 joule m^{-2} s^{-1} respectively. The temperature interval of the isotherm chosen was about 58.5 - 59.5°C. Cf text. Symbols as in tg 1.





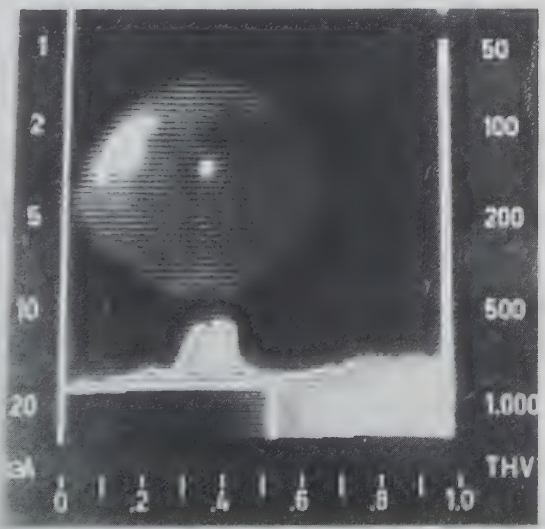
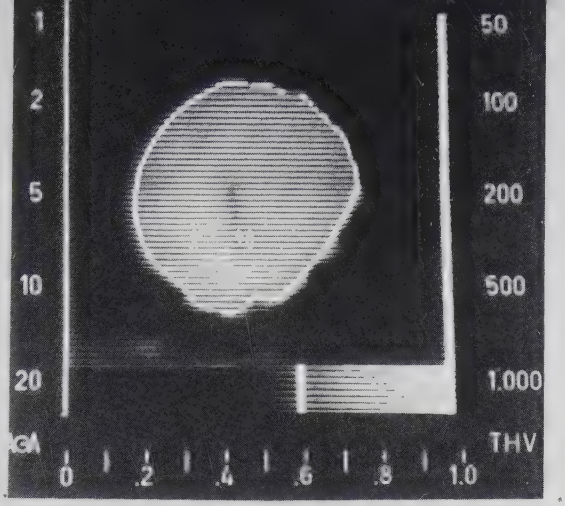


Fig. 5:9. The effect on leaf temperature of a simulated temperature sensor attached to the leaf surface. The leaf was placed in leaf position 5 and irradiated with 2600 joule m^{-2} s^{-1}. The temperature interval of the isotherm chosen was about 39.7 - 40.9°C. Cf text. Symbols as in fig 1.



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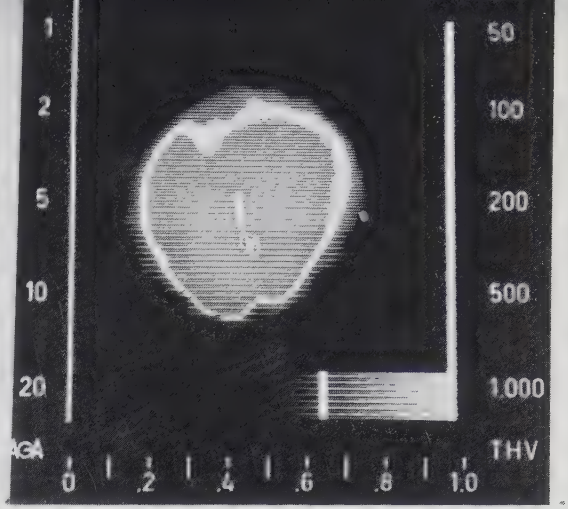

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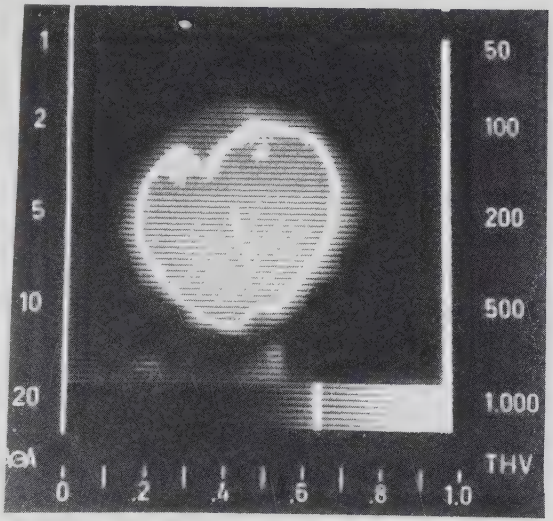

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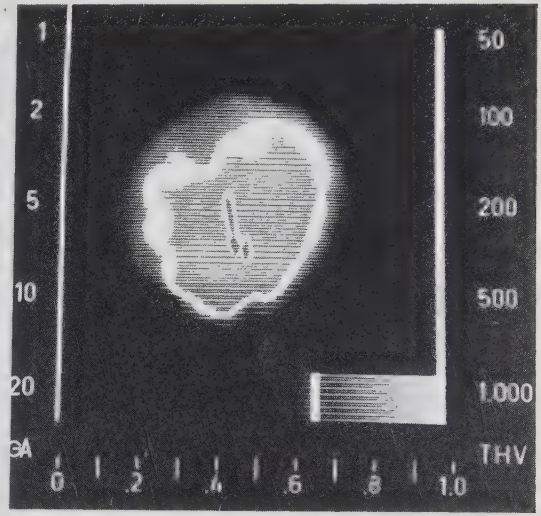

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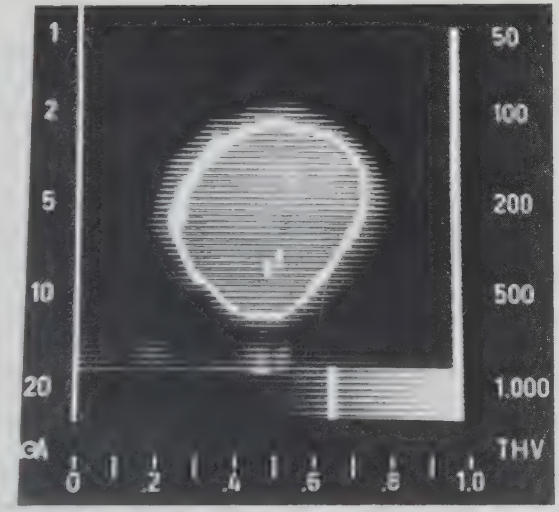
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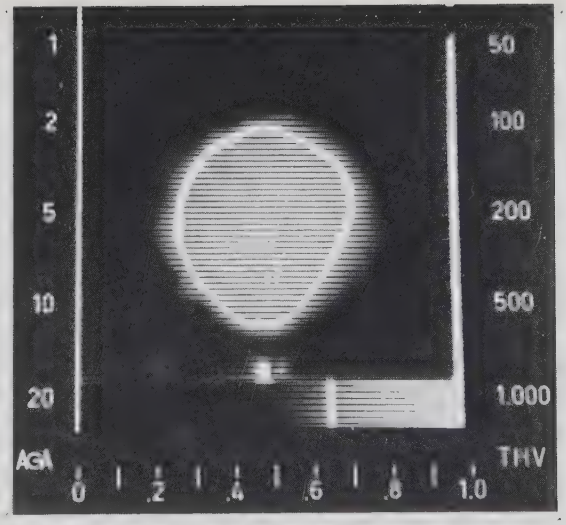
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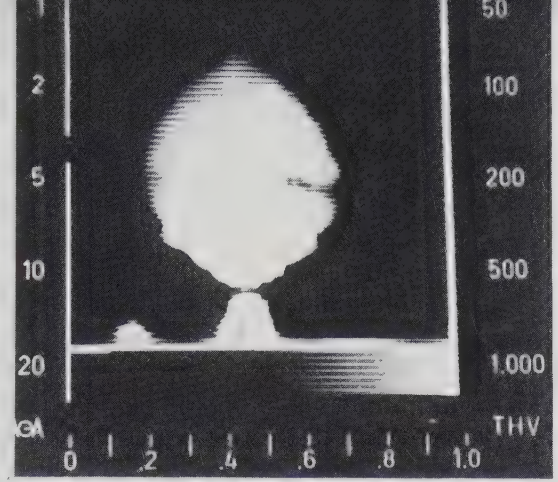

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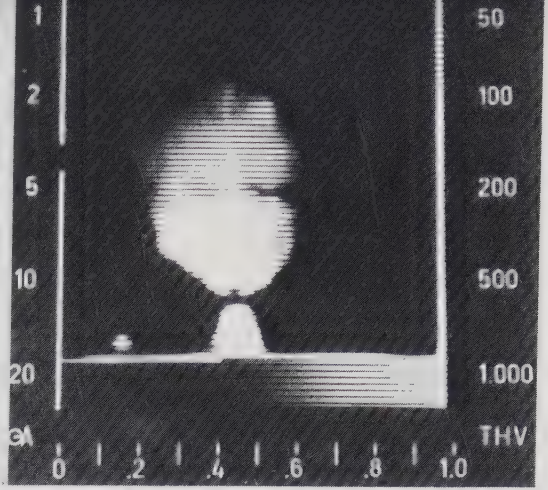

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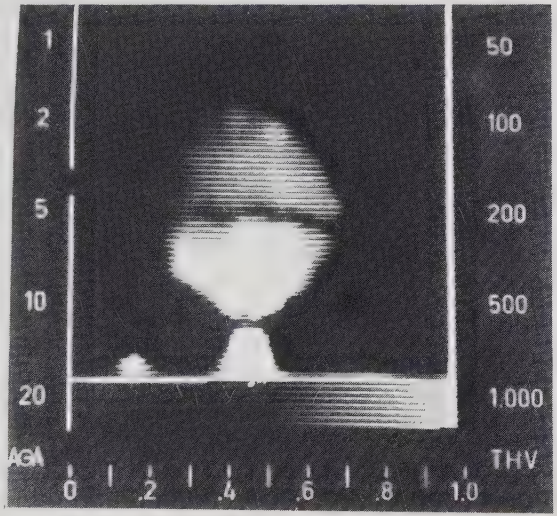

tg 5:3

tg 5. The effect on leaf temperature of wounding a leaf. The leaf was placed in leaf position 5 and irradiated with 2660 joule m^{-2} s^{-1}. Cf text. Symbols as in tg 1.

III.

THERMOGRAPHIC MEASUREMENTS OF THE TEMPERATURE OF SMALL BIRCHES IN THE FIELD.

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ABSTRACT

The temperature of small birches was measured by thermography (Thermovision 680/102 B, AGA AB, Sweden) during the day at a mountain moor locality about 800 m above sea level (Storhogna, Härjedalen, Sweden) in July and August and in a locality of similar appearance at sea level in July (Alnön, Medelpad, Sweden).

Radiation was found to be the most important factor affecting the temperature of the birches. Wind had a lesser influence. At Alnön, the temperature of the leaves facing the sun was high, indicating that leaf position is important to the temperature of the leaf, but at the mountain locality leaf position was found to be of less importance.

During the day, a temperature gradient existed in the different parts of the birch. The leaves were warmer towards the edges (the maximum temperature) and cooler in the centre (the minimum temperature). During the night, a temperature gradient in the birch at sea level still existed, but none in the mountain birch. The difference is thought to be due to increased reradiation at the mountain site. The thermal response of the birch at Storhogna to changes in weather conditions (incoming radiation) was sluggish in August, compared to July, and the temperature gradient was also less pronounced in August than in July.

The ground acts as a heat sink in the morning and as a heat storage and supply center in the evening and early night. When the ground is warm, a warm air layer lies just above it, but this layer disintegrates in the evening when reradiation increases in relative significance. In the morning and evening, warm water from the ground was conducted in the birch at least at Alnön, warming its interior.

The procedure of measuring the temperature of plants in the field by thermography is discussed and modifications suggested.

INTRODUCTION

The important processes governing the heat exchange and consequently, the temperature of a plant are radiation, convection, transpiration and conduction. Other processes are involved in the heat exchange of the plant, but are of minor importance and will not be considered here.

According to Geiger (1973), radiation is the major factor of heat exchange. Reradiation in also important. Both solar and terrestrial radiation affect the plant. Nearly all wavelengths of radiation shorter than about 4.0 µm come from direct solar radiation. Terrestrial radiation, or reradiation, is made up of wavelengths longer than about 3.0 µm (Rosenberg 1974). In other words, reradiation from the plant, the soil and other objects is longwave or heat radiation. The sun, the sky, the clouds, the plant and objects near the plant constitute a complicated radiative exchange system. The plant and the soil radiate nearly as black bodies (Gates 1962, Gates and Tantraporn 1952). Liquid water also radiates nearly as a black body (Kreith 1958, Hsu 1963, Slatyer 1967) and even in thin films absorbs heat radiation very effectively (Trichett and Goulden 1958). The sky radiates as a black body (Gates 1962). Clouds acts as a sort of radiation blinds, shutting out the radiation of the sun and conserving the long wave radiation from the earth; in both cases, reradiation of heat from the clouds increase. Heat always flows from warmer to cooler areas in the thermal environment.

Heat transfer by convection and transpiration depends on the wind velocity, the humidity and temperature of the ambient air, the structure and temperature of the leaf, the entire plant and objects near the plant. In still, hot weather, heat turbulence (free convection) lift hot air bubbles from the ground, which increases the air turnover near the ground (Lowry 1972).

Of the different heat transfer mechanisms mentioned, which one is the most important depends upon the elevation above sea level and the time of the year. Presumed rapidly changing thermal patterns of the plant, due to changes in weather conditions, has to be recorded for the whole plant and its surroundings with a temperature measuring system capable of registering these changes.

The thermal pattern of small birches was studied by thermography (AGA Thermovision System 680/102 B, AGA AB, Sweden) in one day experiments each in July and August at a mountain moor location in Härjedalen

and one in July in Medelpad. A mountain moor locality about 800 m above sea level and a similar appearing locality at sea level were chosen. Since the thermal pattern of the plant and its surroundings may be different at different times of the year, the mountain moor locality was revisited in late summer.

MATERIAL AND METHODS

Small birches were studied at Storhogna (figures 1 and 3) and at Alnön (figure 2). The birch at Storhogna grew above the timber line in a stony mountain moor location. The birch at Alnön (at sea level) grew in a deserted, rather flat, vast gravel pit with a south west exposure. The localities were chosen because they resembled each other in physical appearence.

In July, the birch at Storhogna had 26 leaves and was 14 cm tall (maximum length 16.3 cm) with a diameter of about 5 cm. The maximum and minimum temperatures and, at certain periods of the day, the medium temperature of the birch were recorded. The calculated difference between the maximum and minimum temperature and the corresponding thermal picture, or thermogram, of an object, we called the "medium" temperature. The temperature of three leaves was also recorded (figure 1, A,B and C).

The birch at Alnön had 23 leaves and was 18.5 cm tall with an average diameter of 4 cm. The maximum, minimum and at certain periods of the day the medium temperature of this birch were recorded.

The birch at Storhogna grew a little during the weeks between July 17th to 18th and August 15th. The height of the birch became 15.5 cm (length 17.7 cm) and the mean diameter about 5.5 cm.

Thermography was used to study the temperature of the birches; the equipment consisted of a Thermovision 680/102 B - set (AGA AB, Sweden) with the infrared camera placed about 1 m from and at the same level of the birch (cf figures 1, 2,and 3) and pointing approximately north (380° on the compass). Electric power (220 V, 50 Hz, 300 W) was supplied by a motor-driven electric aggregate (Honda).

First, the temperature of a leaf in the upper, middle, and lower part of the birch was studied (A, B and C in figure 1). This method of measurement was not adequately describing the temperature

Fig. 1. The birch at Storhogna in July. A, B and C indicate leaves measured during the day. The infrared camera is seen in the background. The thermometers are a battery-driven contact thermometer (to the left in the picture) and a mercury laboratory thermometer (to the right in the picture).

Fig. 2. The infrared camera and the birch at Alnön in July. Cf text.

Fig. 3. The birch at Storhogna in August; cf figure 1.

pattern of the object and was consequently, in later investigations, abandoned. In all investigations the maximum and minimum temperature of object was measured in isothermic units from which the true temperature of the object was calculated with corrections for 5 % reflectivity and 0 % transmissivity (Thofelt 1975 b). The medium temperature of the object was calculated and recorded. When there were no temperature differences only one temperature measurement and one thermogram was taken.

The thermal picture of the birch was obscured by the thermal pictures of its surroundings, which made it difficult to distinguish the thermal image of the birch at times when temperature differences between the objects, including the ambient air, were small. So, a thermal "back-ground" screen, made of corrugated paper, a board of wood, and a water-flask, was used during the short period of thermographic recording. The utilities were brought away immediately after the recording of the thermogram. The temperature of the object increased about 0.2 to 0.5°C during this operation depending upon weather conditions.

A mercury laboratory thermometer was used as the known temperature source (or reference temperature). These temperature readings were used as the temperature of the ambient air (cf Thofelt 1975 b). A contact thermometer can be seen in figures 1 to 3 but the readings of this thermometer differed more from the ambient air temperature than the temperature readings of the mercury laboratory thermometer measured with Thermovision 680.

Incoming radiation was measured with a silicon photovoltaic cell mounted horizontally about 1 meter from the birch (cf Thofelt 1975 a,b). Humidity of air was measured with a hair hygrometer (Lamprecht) placed upright on a paper box 0.8 meter from the birch, and covered with the longitudinal half of a plastic tube ("frigolite") about 20 cm in length in order to protect it from the direct rays of the sun. Wind speed was measured with a hot wire anemometer (Fuess, Berlin) at ground level, 0.5, 1 and 2 meter above ground level. The probe was held perpendicular to the direction of the wind.

All instruments were read every 20, 30 or 60 minutes depending upon the time of day and weather conditions. When there were changes in the thermal picture the recordings were more frequent.

Abbreviations and symbols

S1	Storhogna in July.
A	Alnön in July.
S2	Storhogna in August.
I	Incoming radiation in joule m^{-2} s^{-1}.
W,$\tilde{W}$	Wind velocity and mean wind velocity in m s^{-1} respectively.
⬆	The direction of the wind in relation to the points of the compass:
m a g	Meter above ground level.
t	Temperature in °C.
t_a	Temperature of the ambient air in °C.
RH	Relative humidity in %.
VPD	Vapor pressure deficit in 10^2 K Pa (approximated from values in g water m^{-3} air (cf Geiger 1973).
TD	Time of the day (h).
THV	Thermovision 680/102 B (AGA AB, Sweden).
tg	Thermogram or the recorded thermal picture of the object.

The abbreviations in the thermogram are as in the examples:

S1:0500	The thermogram was taken at Storhogna in July at 0500 hours representing small or no temperature differences in the object.
S1:1100:AA (MIN,MED,MAX)	The thermogram was taken at Storhogna in July at 1100 hours representing the temperature of the ambient air (the minimum, [illegible] object respectively).

WEATHER SYMBOLS:

	Rain.
	Fog, mist and clouds.
	Clear sight but cloudy weather.
	Changing clouds.
	Sunshine.
	Clear weather but no sunshine.

RESULTS

The results will be presented in order: Storhogna in July, Alnön in July and Storhogna in August.

STORHOGNA IN JULY.

Weather conditions at Storhogna in July are shown in figure 4. Incoming radiation, temperature and relative humidity of the ambient air, and vapor pressure deficit during the day are found in figure 5. Wind velocities at 0, 0.5, 1, and 2 meters above ground level are shown in figures 6 - 9. Figure 10 shows the temperature of leaves A, B and C (see figure 1) and figure 11 the maximum, medium, and minimum temperature of the birch.

When incoming radiation was low, the temperature of the birch was low and no temperature differences existed between the different parts of the birch. With increasing radiation, the temperature of the birch increased, (see S1:0300 - 0840) and the difference in temperature between the different parts of the birch increased (see S1:1140, 1340 and 1420). When radiation intensity decreased in the afternoon, the temperature of the birch and the difference in temperature between its different parts decreased. When radiation intensity was very low, the temperature of the birch was low and was equal to that of its surroundings (see figure 10 and 11).

Wind velocity did not affect the temperature of the birch as much as radiation did. When wind velocity increased, the temperature of the birch dropped (see, for example, S1:1540 and figures 6 - 9). The influence of wind compared to radiation was small.

In the morning, the temperature of leaves A, B and C was close to the temperature of the ambient air, with leaf C, the one nearest the ground, being the warmest of the three. In the afternoon, the leaves at the top and the bottom of the birch were the warmest (see figure 10). The middle leaf was the coolest in the afternoon, especially during a period of increased wind velocity beginning at 1540 hours.

In the morning the temperature of the birch was below that of the ambient air (see figure 11 and S1:0300 to 0800). In the later forenoon temperature differences between different parts of the birch appeared and its maximum temperature was higher than the ambient air. Later on these differences disappeared, also the leaves and the air

were the same temperature. In periods of strong radiation, the maximum temperature was found near the edges of the leaf, with the ambient air of the same temperature, "enveloping" the birch (see for example S1:1420:MAX). When the birch cooled in the afternoon, its maximum temperature was found farther from the leaf edges (see for example S1:1730:MAX).

The minimum temperature of the birch was well below the temperature of the ambient air (see figure 11) and was usually found near the centre of the leaf (see for example S1:1420,1540:MIN). In periods of strong insolation, the difference between the maximum and minimum temperature of the birch was greatest (cf figure 11 and S1:1420).

In the morning, the ground gradually warms and at about 1040 is very warm compared to the birch (see the gray tones in S1:1040). In the afternoon, the surface of the ground gradually cools as indicated by the darkening gray tones of the thermograms (see for example S1:1040 to 1730, all MAX). In the evening, the surface is even cooler, but the water in the ground still seems to be warm.

The temperature of the birch may also be influenced by the inflow of water from the ground. In the evening, the stem of the birch was warmer, as indicated by the gray tones of the thermogram (S1:1730:MAX, 1800 to 2100). The inflow partly explains the fact that the temperature of the birch is lower than the ambient air in the morning and higher in late afternoon.

When the temperature of the ground increases, the temperature of the ambient air increases (see figure 11 and the gray tones of the thermograms of the morning hours). In the morning, the air near the surface of the ground is divided into two layers which are stable during the day and disintegrate in the afternoon (cf S1:0940 to 173[illegible], all marked AA). At 1540 hours, these two air layers were disturbed, probably due to increased wind velocities (see figures 6 - 7). Of the two air layers, the lower one has the higher temperature.

As a general outline of the thermal pattern of the birch during the day, there is warming in the morning and forenoon by radiation (solar and terrestrial) and inflow or warm water from the ground. In the afternoon, the birch gradually cools due to decreasing solar radiation, reradiation, and to a lesser degree, transpiration. In the evening, the importance of reradiation from the birch increases because of very low solar radiation levels and the disintegration of the warm air layer near the ground. To a certain degree, the heat

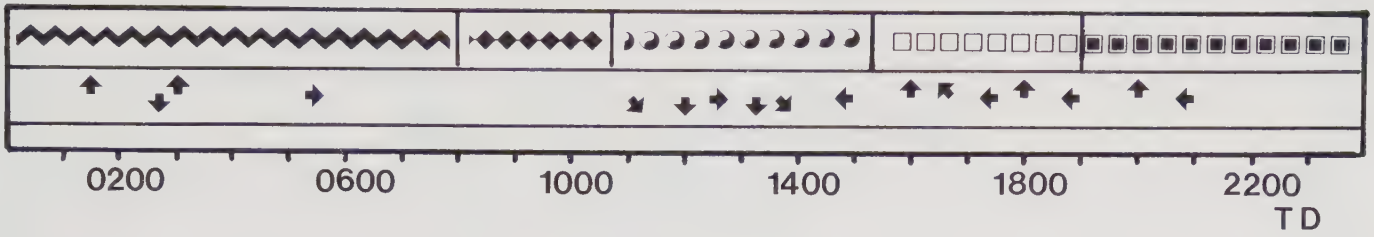


Figure 4. Weather conditions at Storhogna in July (cf abbreviations and symbols!).

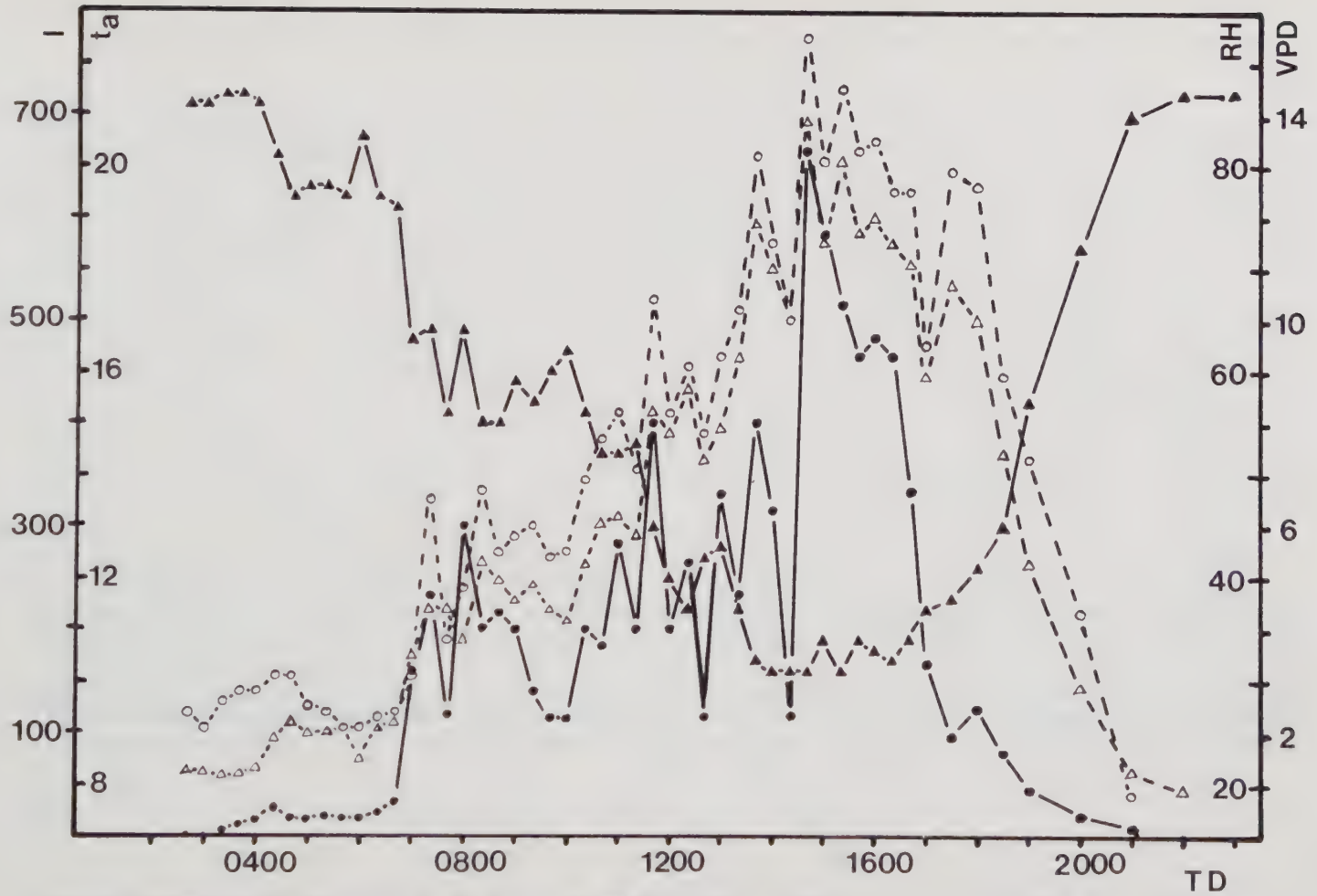


Figure [illegible] and VPD (Δ----Δ) during the day at Storhogna in July (1: [illegible]).

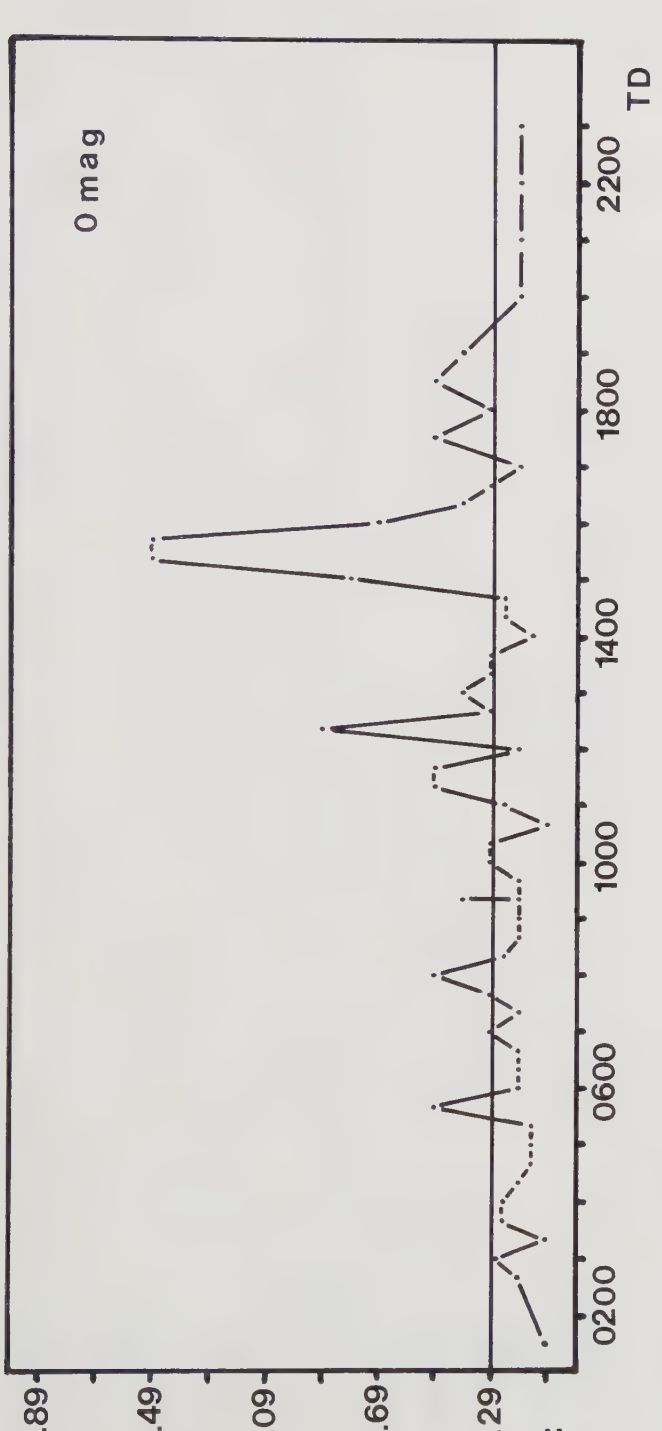
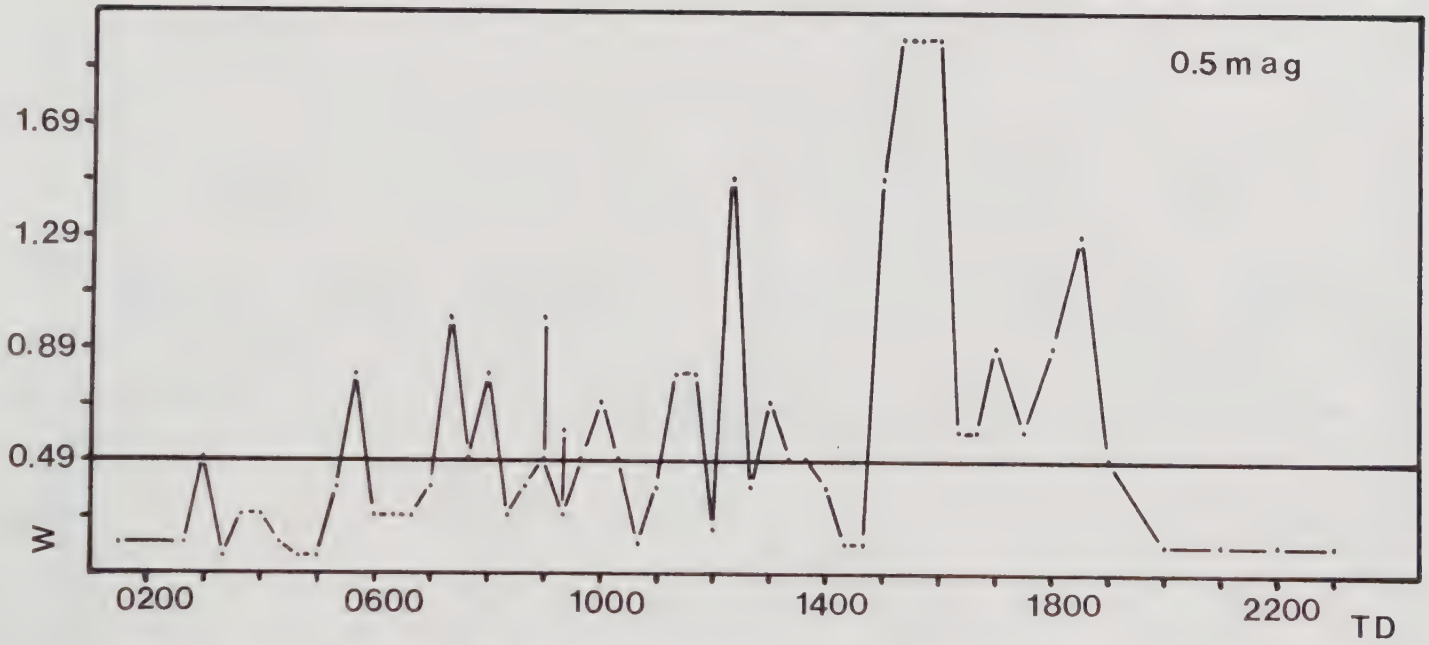


Figure 6. Deviations between the wind velocity from the mean wind velocity ($\bar{W}$ = 0.29) at ground level at Storhogna in July. Cf figure 5.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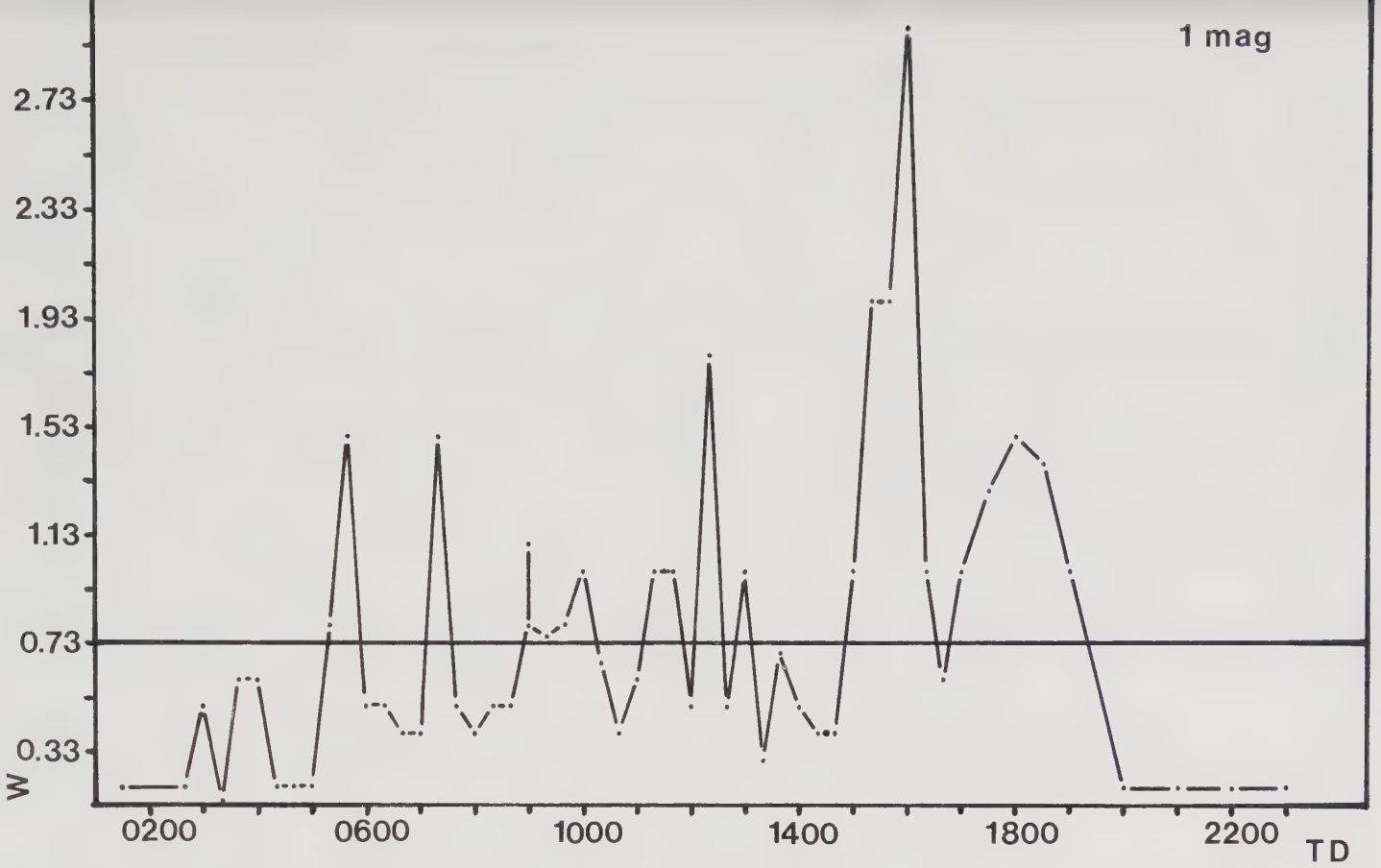
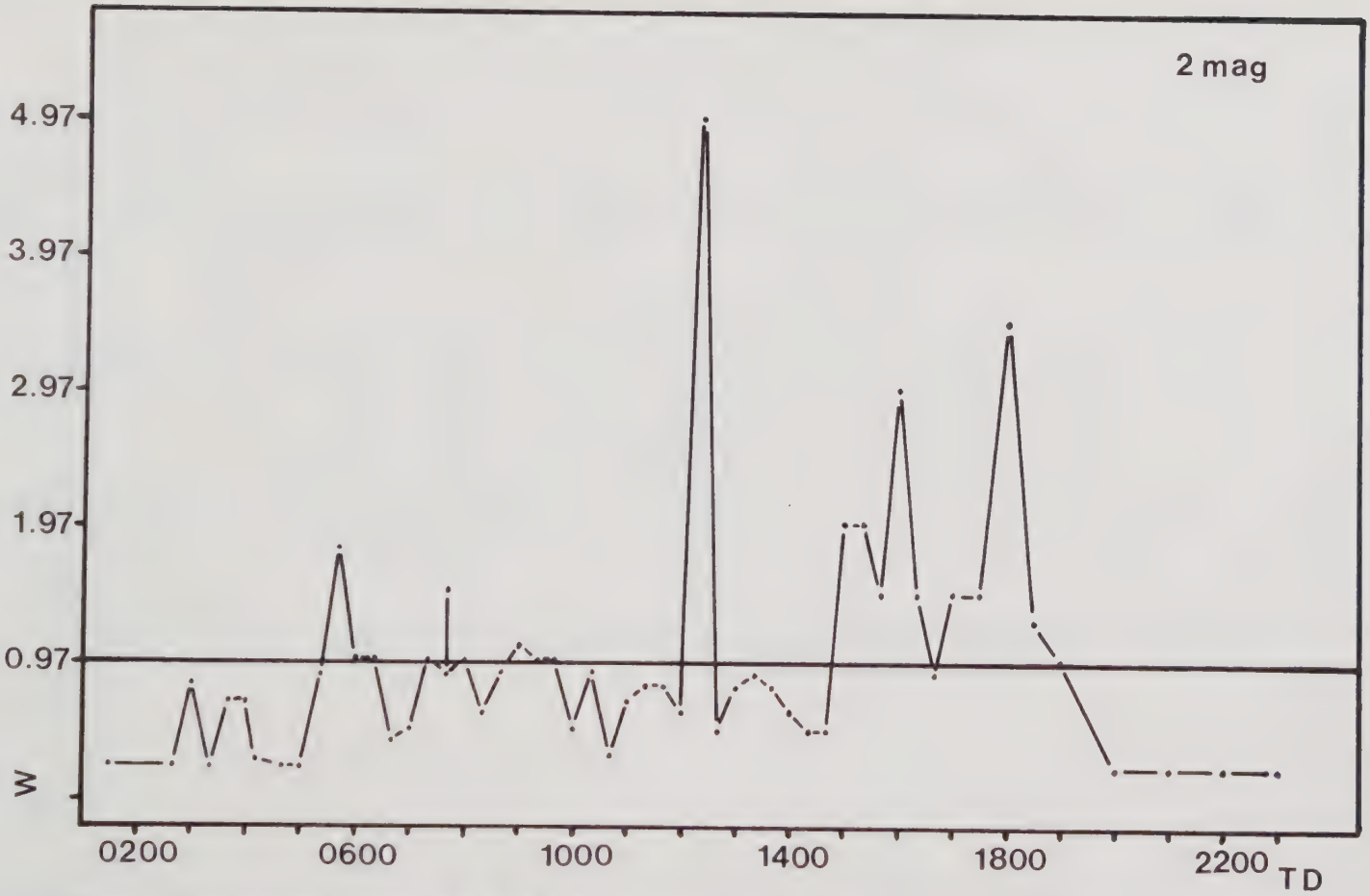


Figure 8. Deviations between the wind velocity from the mean wind velocity ($\bar{W}$ = 0.73) at 1 meter above ground level at Storhogna in July.



. deviations between the plot velocity from the mean wind velocity ($\bar{W}$ = 0.97) at 2 meter above ground level at Sharjah in July.

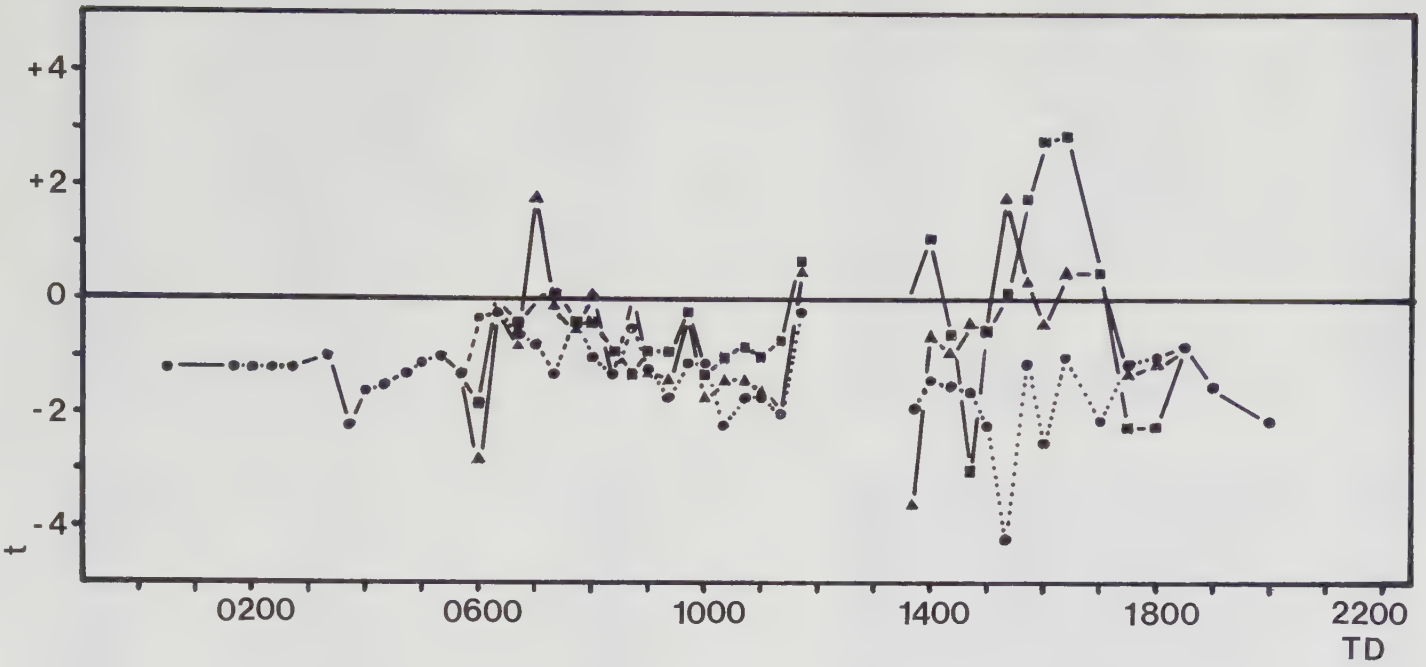
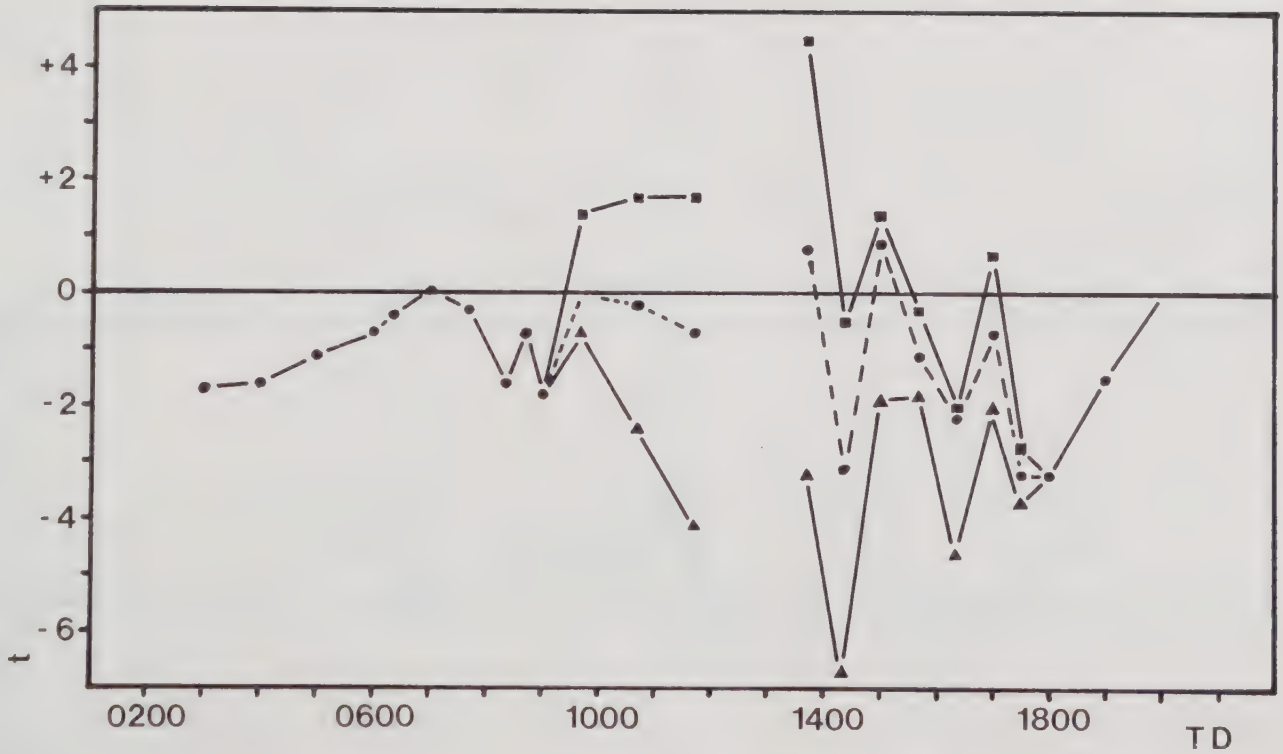


Figure 10. Deviations between the temperature of leaf A (■——■), B (●----●) and C (▲——▲) from the temperature of the ambient air, cf figure 1 and text. The temperature of the birch when even (● —— ●).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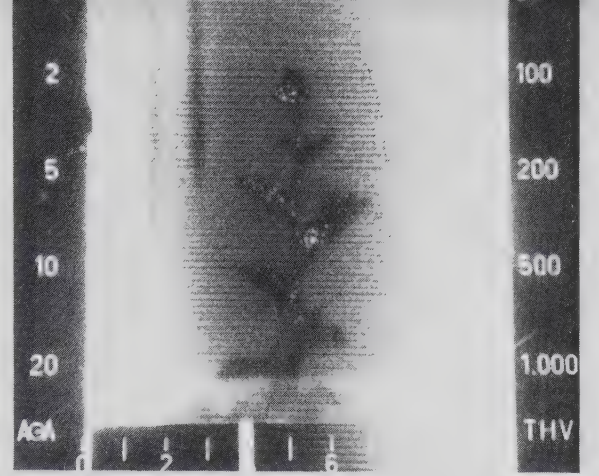

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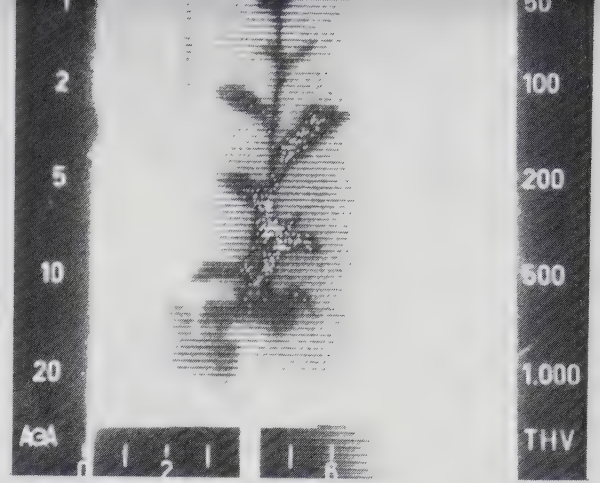

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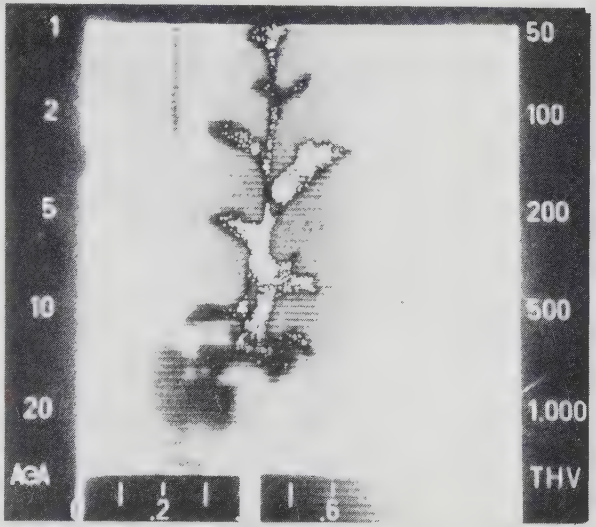

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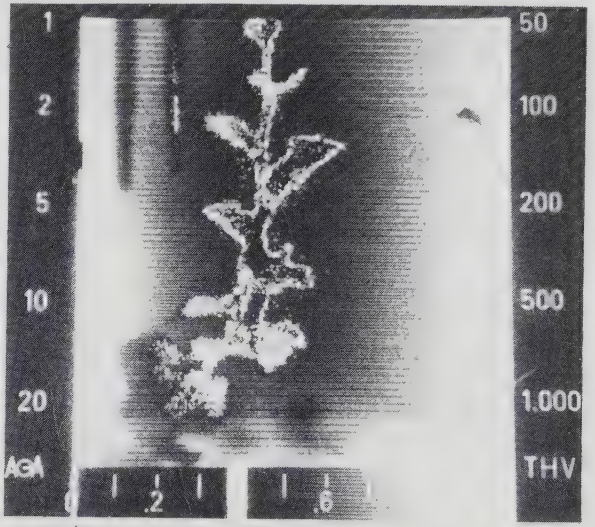

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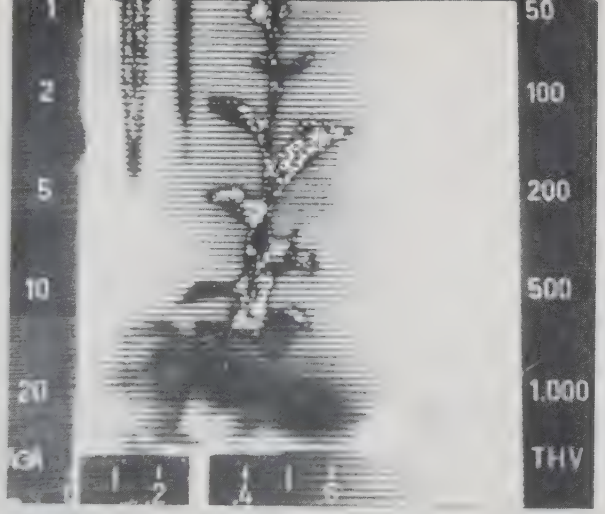
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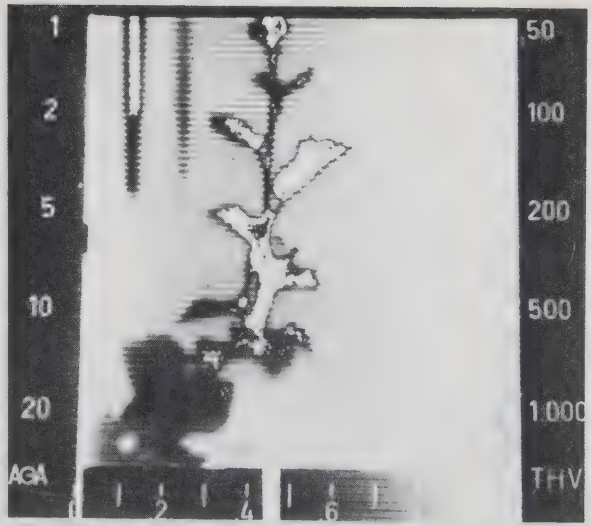
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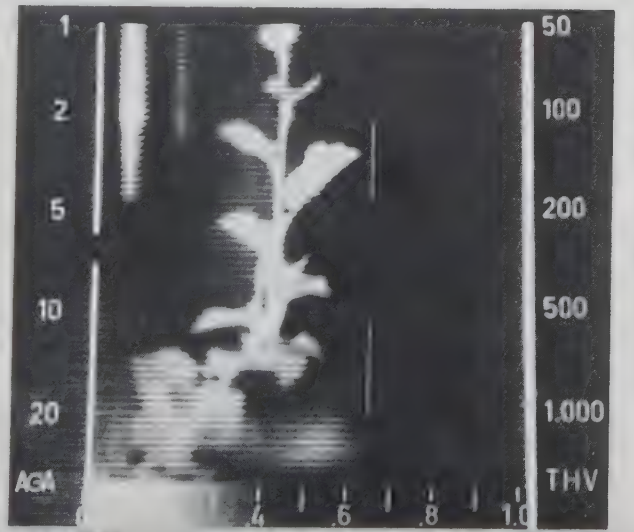
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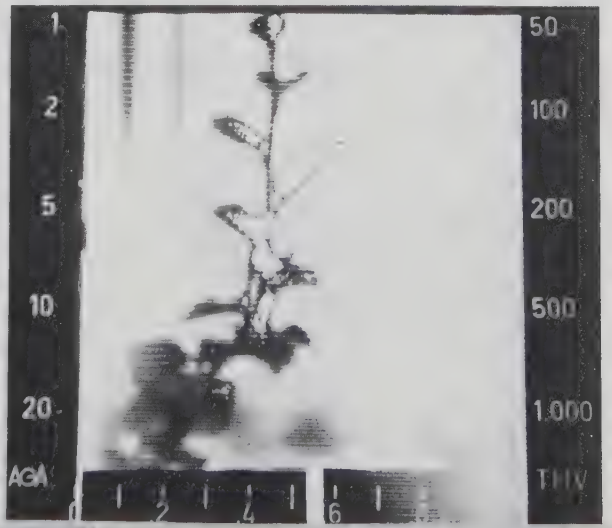
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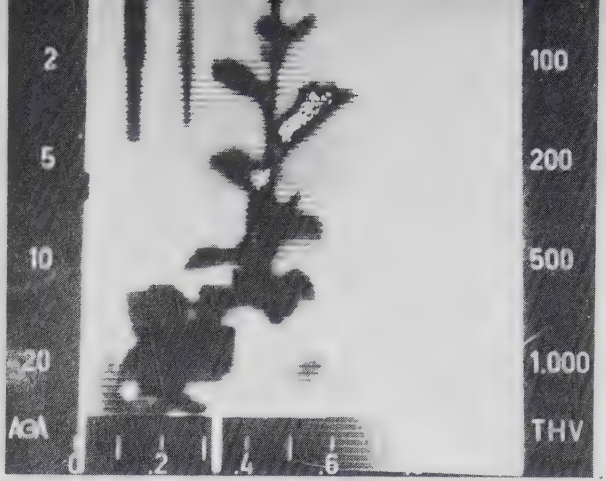

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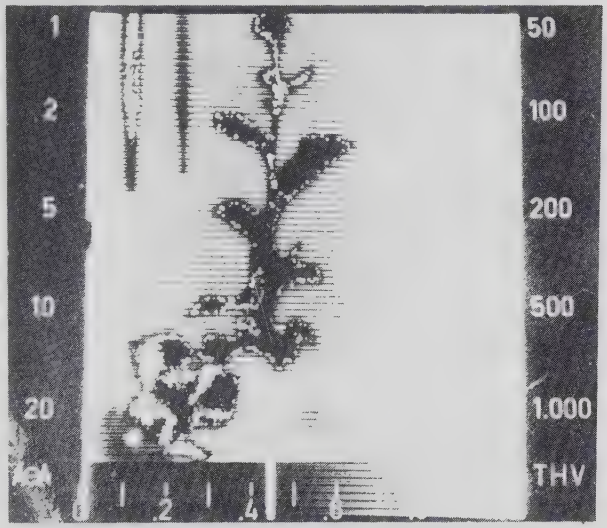

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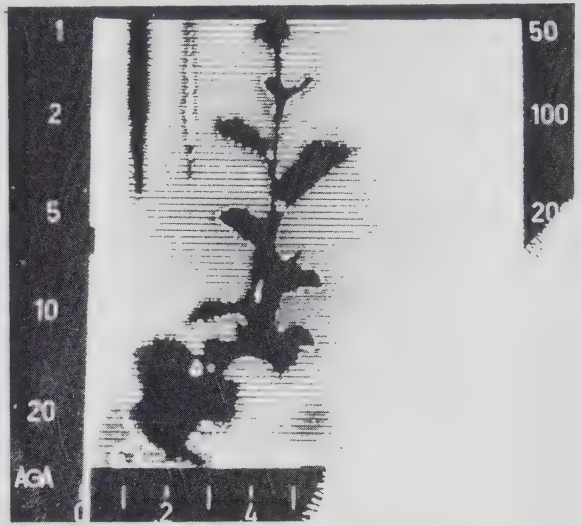

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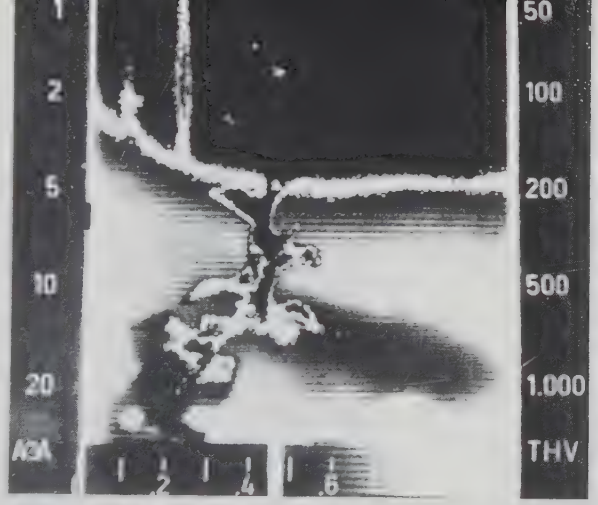
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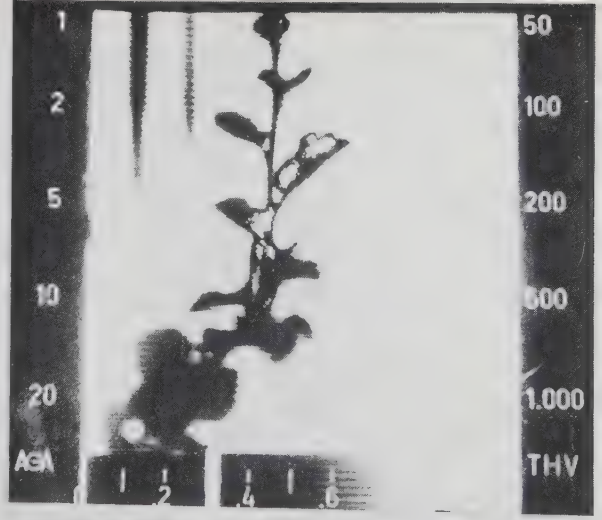
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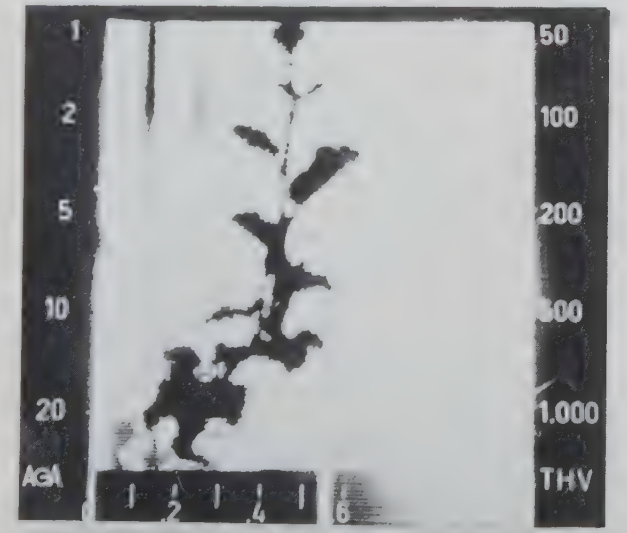
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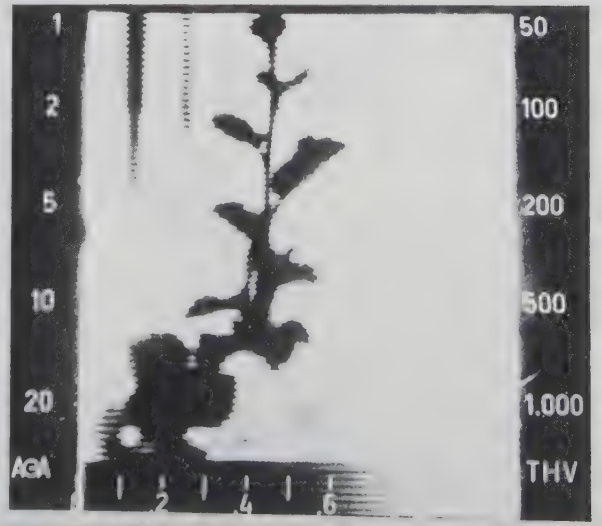
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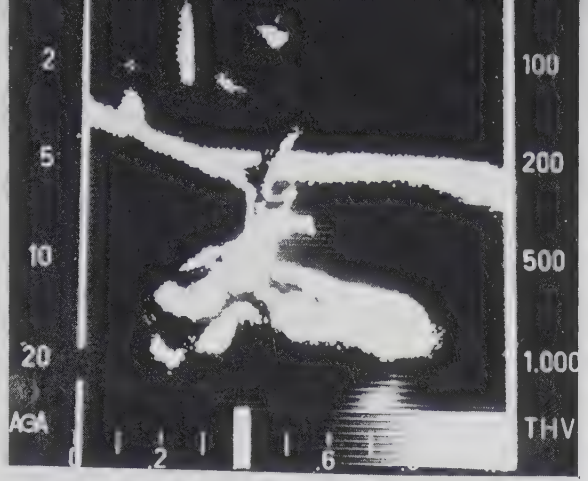

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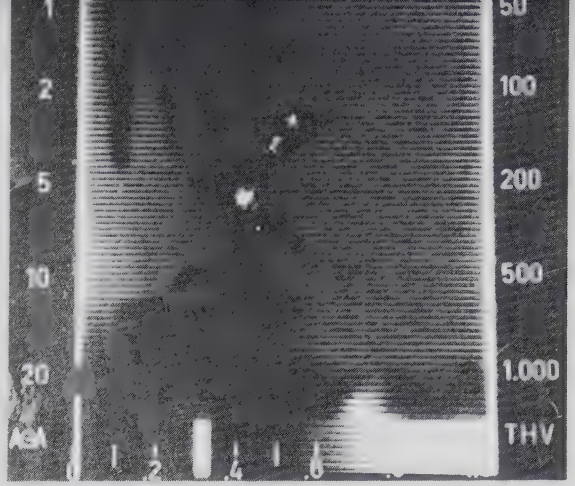

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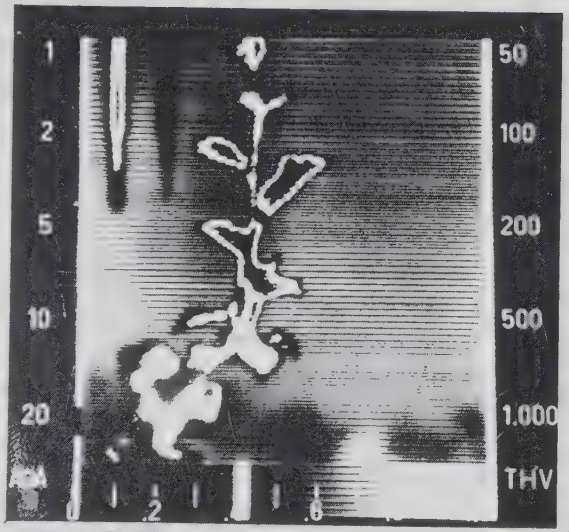

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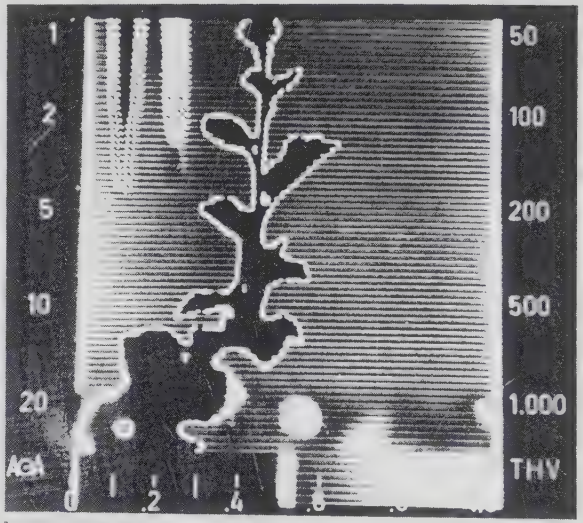

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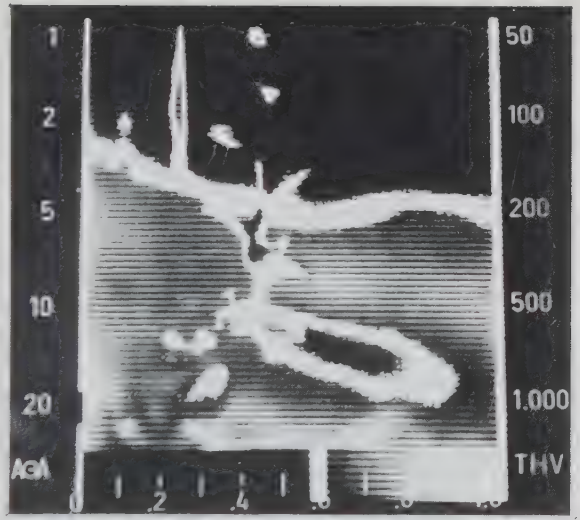
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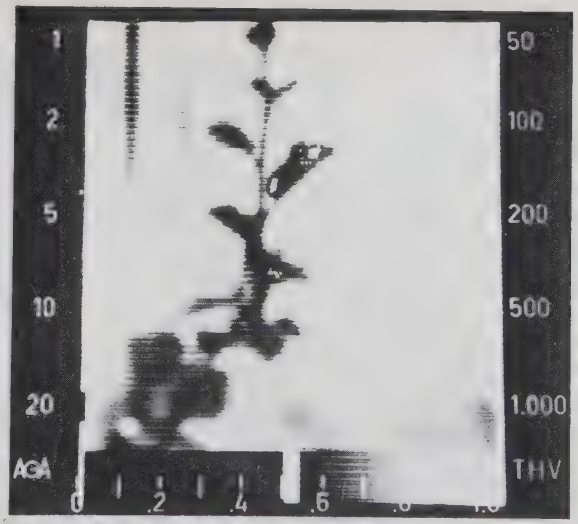
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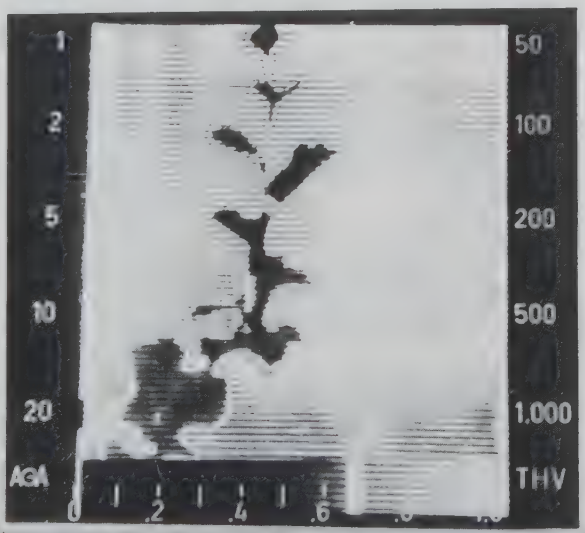
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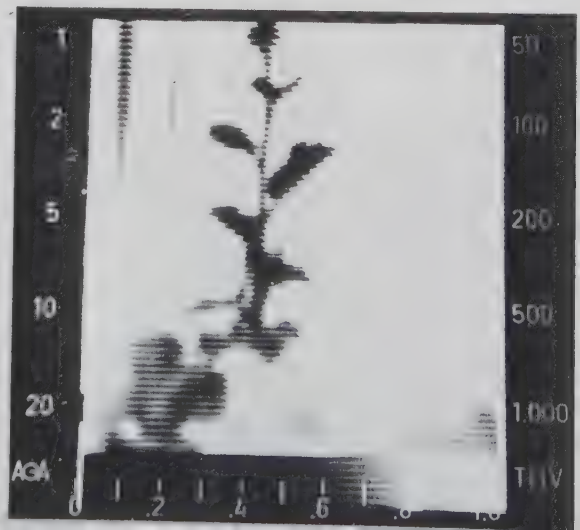
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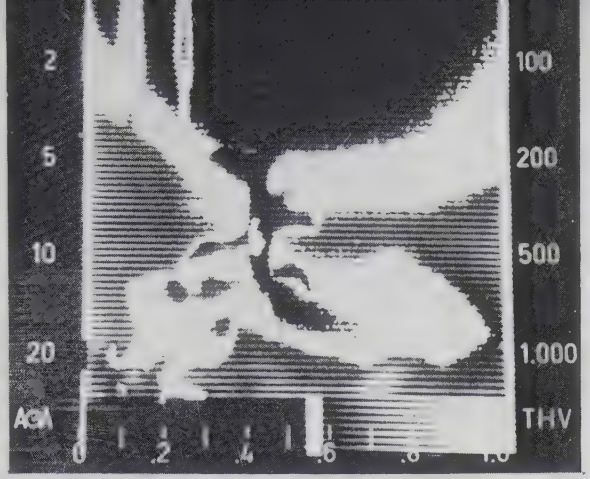

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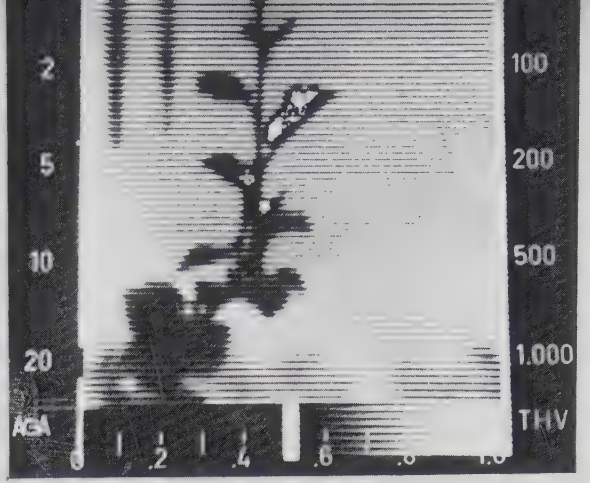

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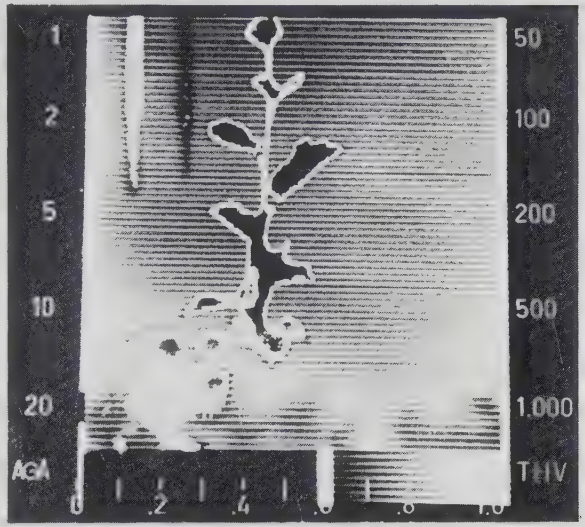

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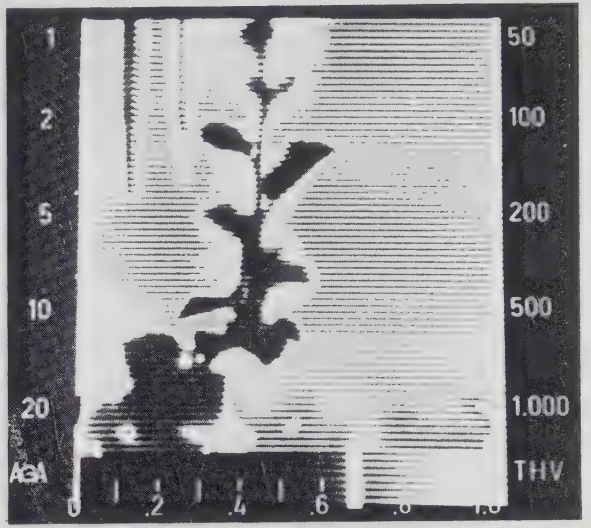

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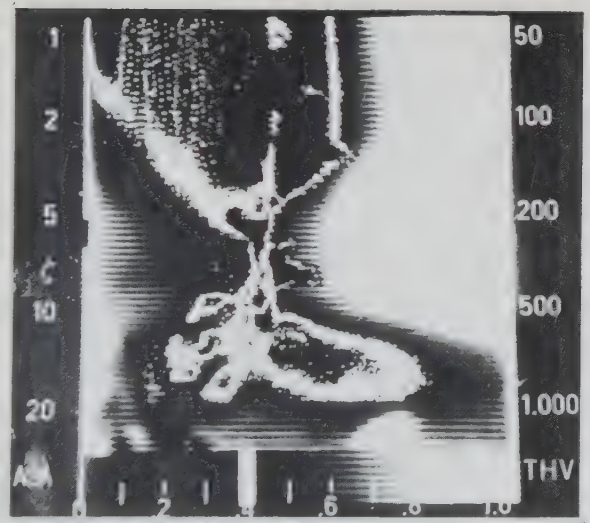
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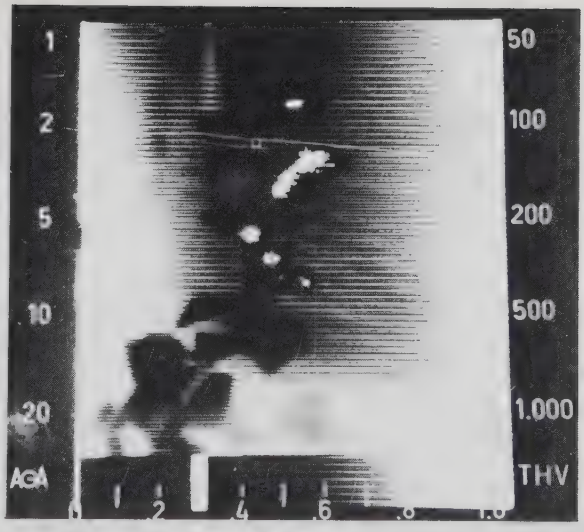
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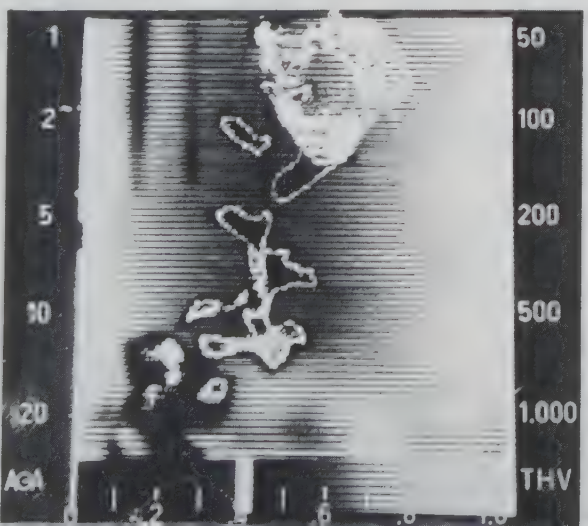
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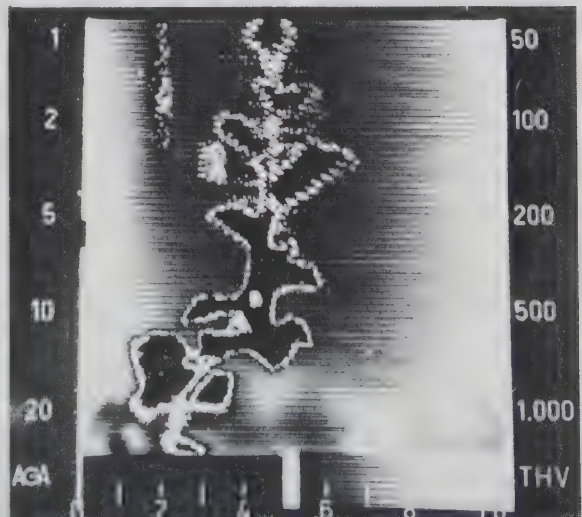
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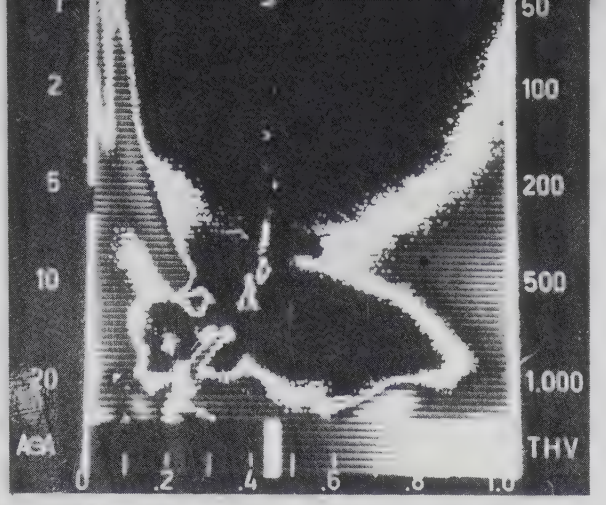

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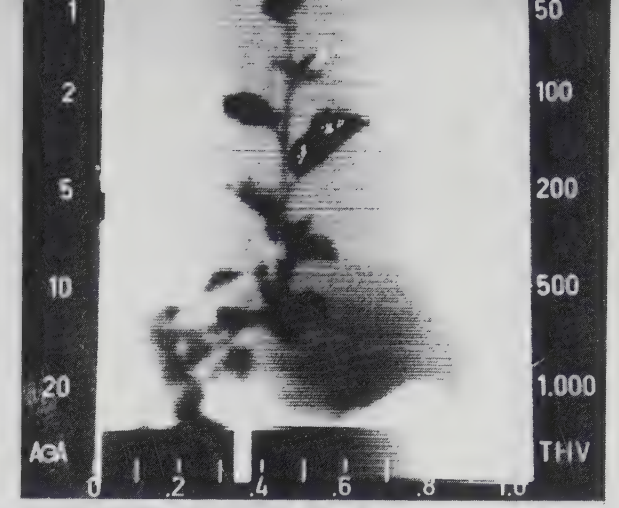

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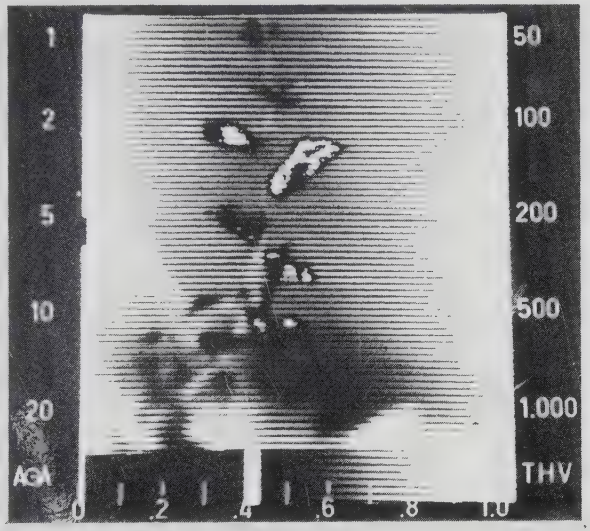

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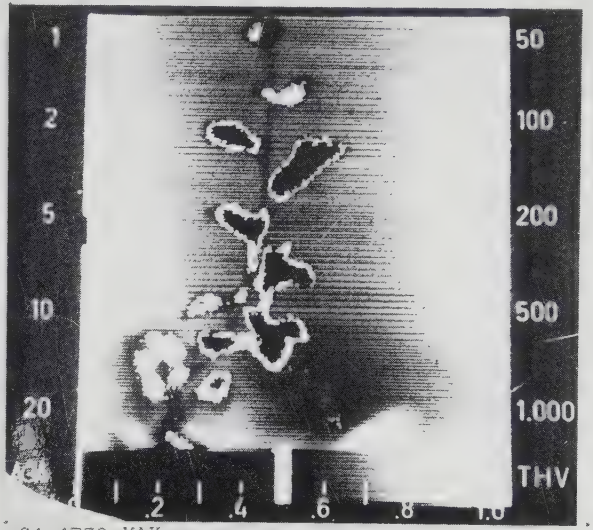

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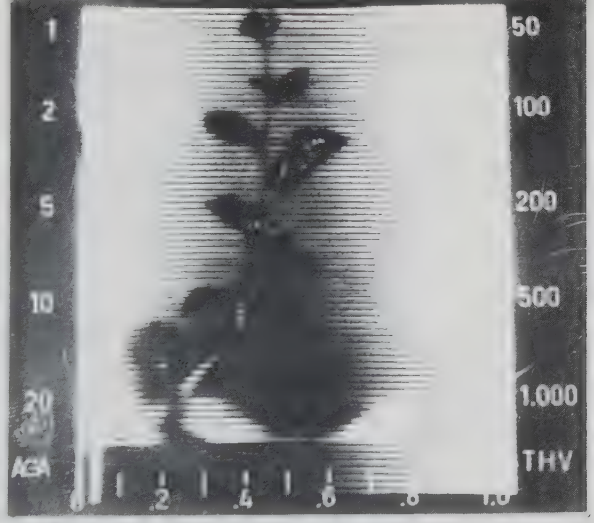
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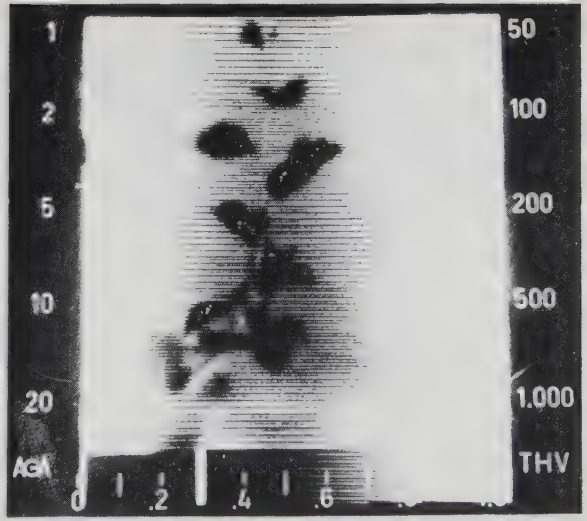
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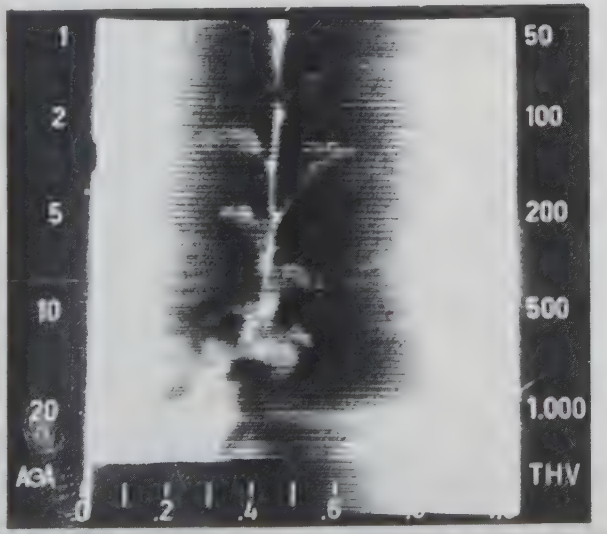
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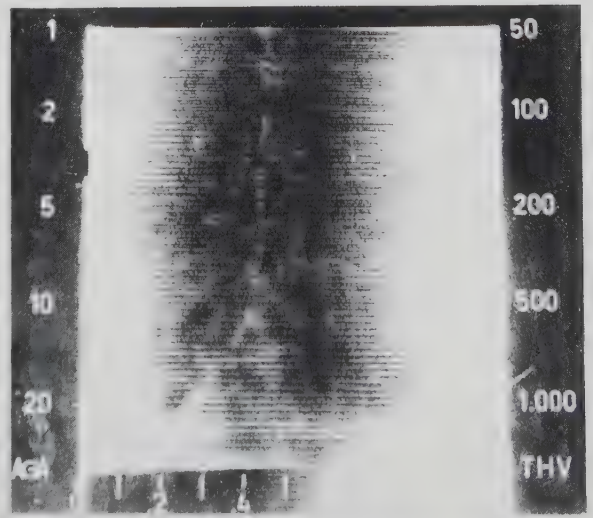
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losses are counteracted by conduction of warm water from the ground into the birch.

The other two thermogram series are similar to the first but there are some differences.

ALNÖN IN JULY.

Figures 12 - 18 show the weather conditions, and the maximum, medium, and minimum temperature of the birch. In the forenoon of the second day at Alnön, the solar radiation was very intense, resulting in a high temperature of the ambient air and the birch. When thin clouds covered the sun, the temperature of the birch immediately fell (see at 1230 hours figure 18 and S1:1230).

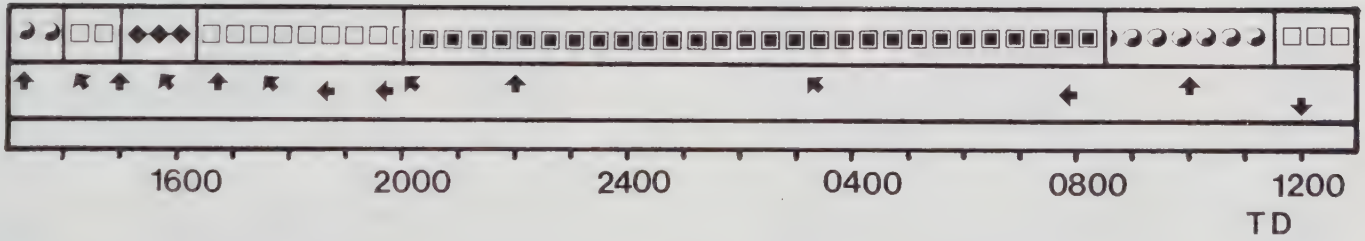
Wind velocity was high in the afternoon of the first day, resulting in the temperature of the birch falling below that of the ambient air. The influence of wind seems to be greater at this locality than at Storhogna (cf figures 14,15,18).

Leaf position influenced the temperature considerably (A:0930, 1300). Leaves perpendicular to incident radiation (to the left in the thermograms) were very warm, as indicated by the gray tones.

The maximum temperature of the birch was always about the same as the temperature of the ambient air, exceeding it only in periods of strong insolation (see figure 18 and S1:0930,1300). There was a great difference between the minimum and maximum temperatures during the day and also during the evening and night, which is contrary to the result at Storhogna. This might be due to transpiration, the influence of which on the temperature of the birch increases when the importance of reradiation decreases.

The grass leaves near the birch are cool during the day (cf A:1400,1440) but warm at night (see A:2400, to the left in the thermograms). However, the tussock of grass to the right in the thermograms seems to be warm during the day but cool at night. In the evening of the first day, and in the morning of the second day, warm water was transported through the stem of the birch.

Radiation seems to be of less importance at this locality than at the more intensive radiation regime at the mountain site.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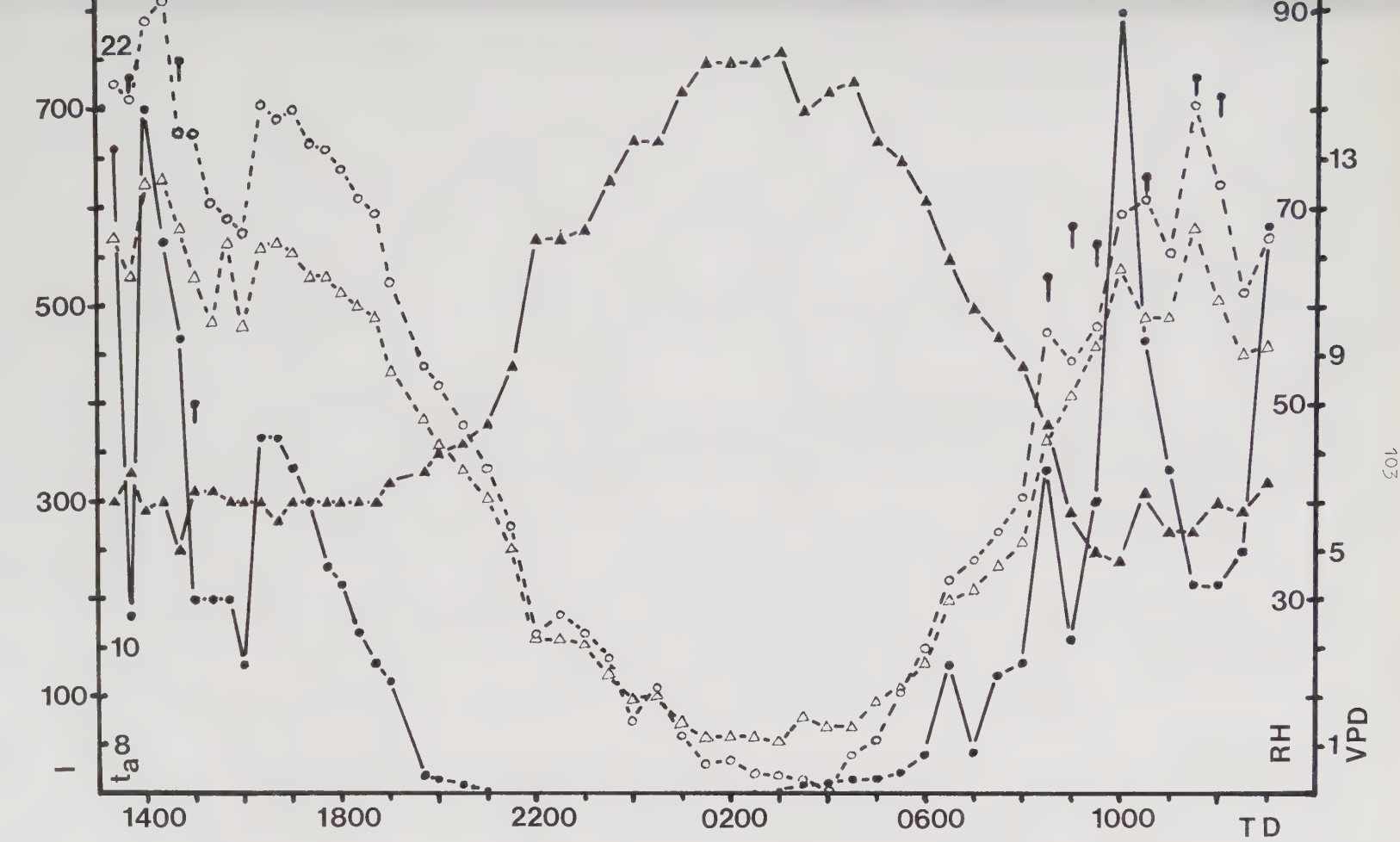
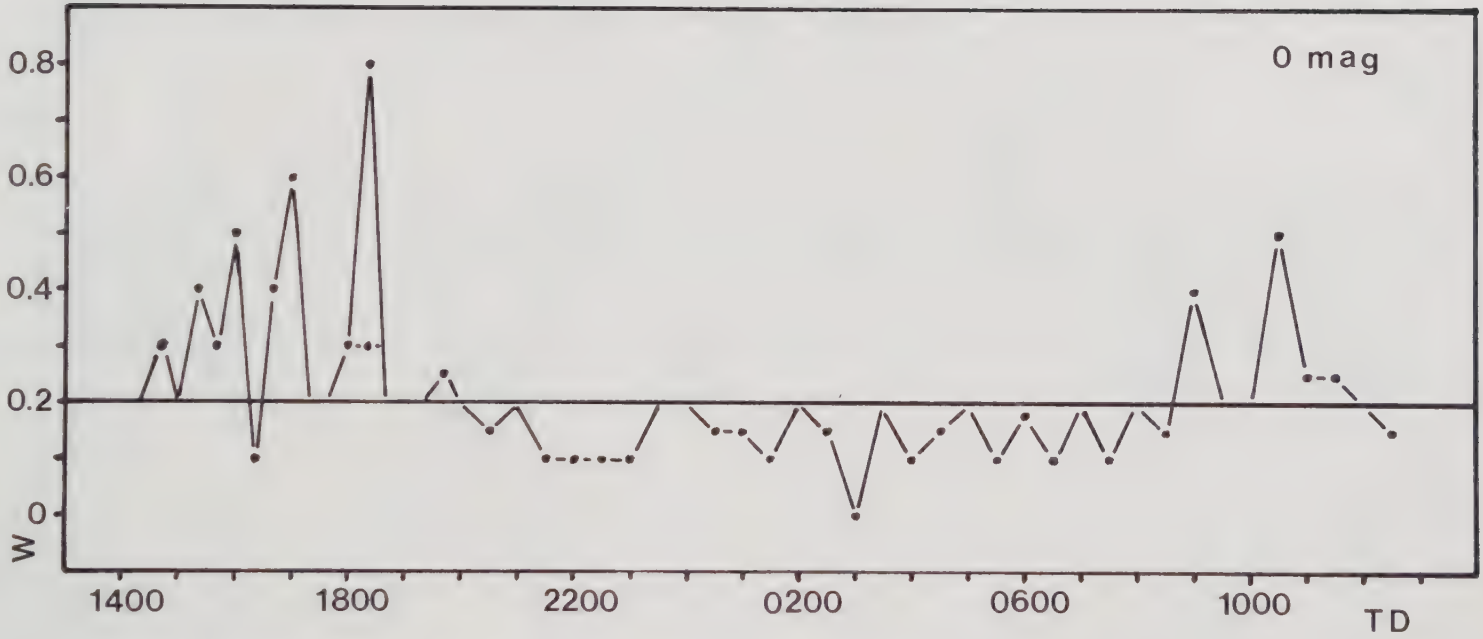


Figure 13. Changes in I (• —— •), t_a (o----o), RH (▲——▲) and VPD (△----△) during the day at Alnön in July. (⍑) indicates the upper value of the measured incoming radiation at the time of the day. (Cf figure 5).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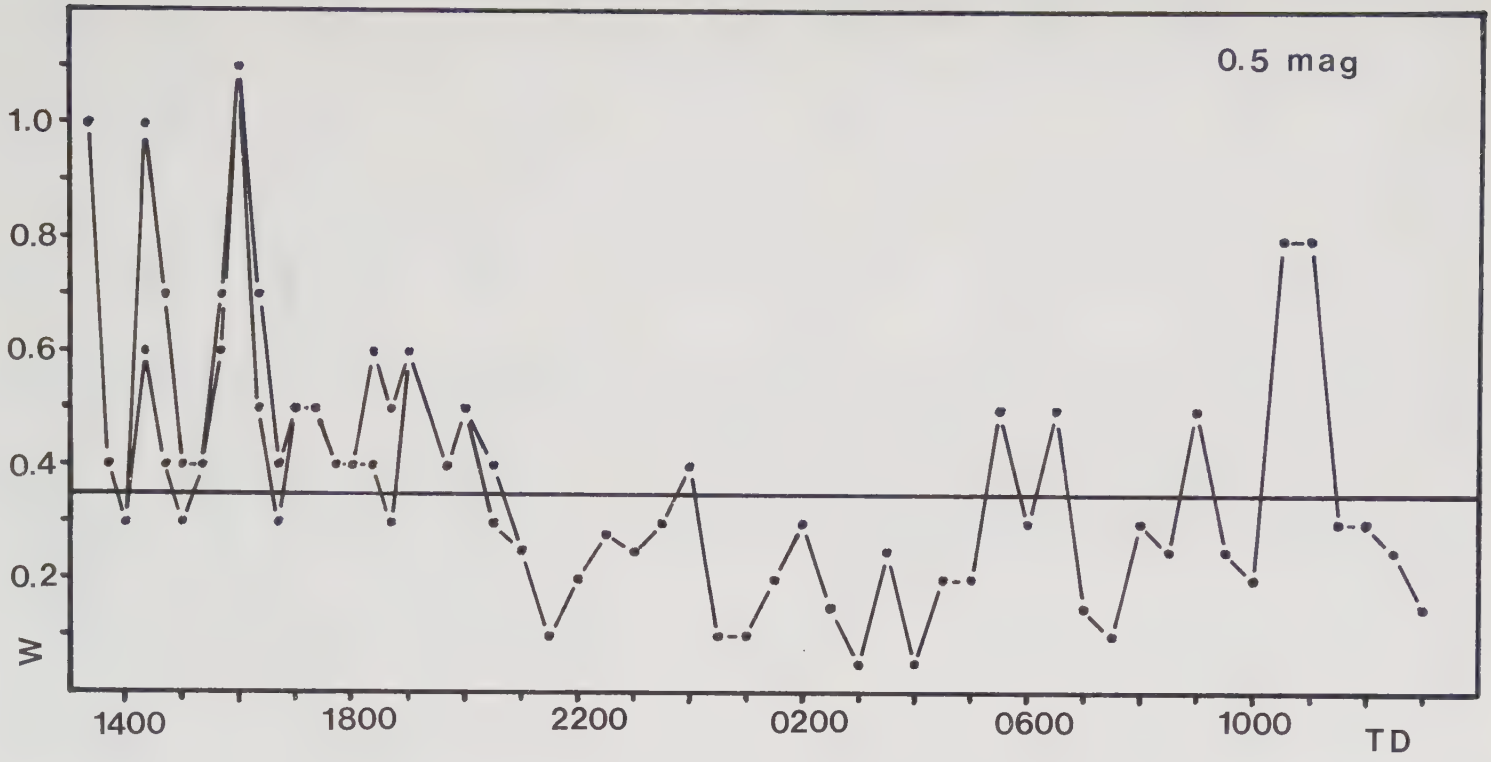
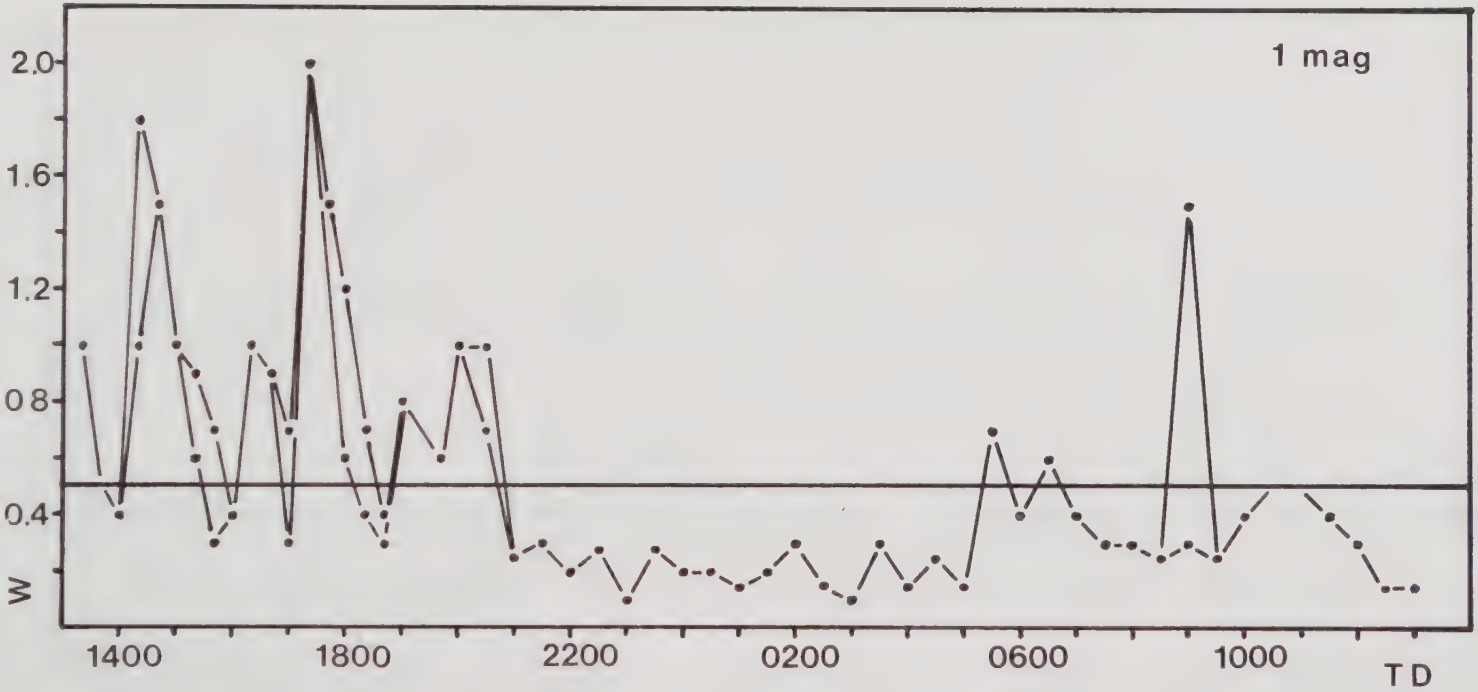


Figure 15. Deviation between the wind velocity from the mean wind velocity at Alnön in July ($\bar{W}$ = 0.35) at 0.5 meter above ground level (cf figure 5).



can wind velocity at Alnön in July ($\bar{W}$ = 0.51) at

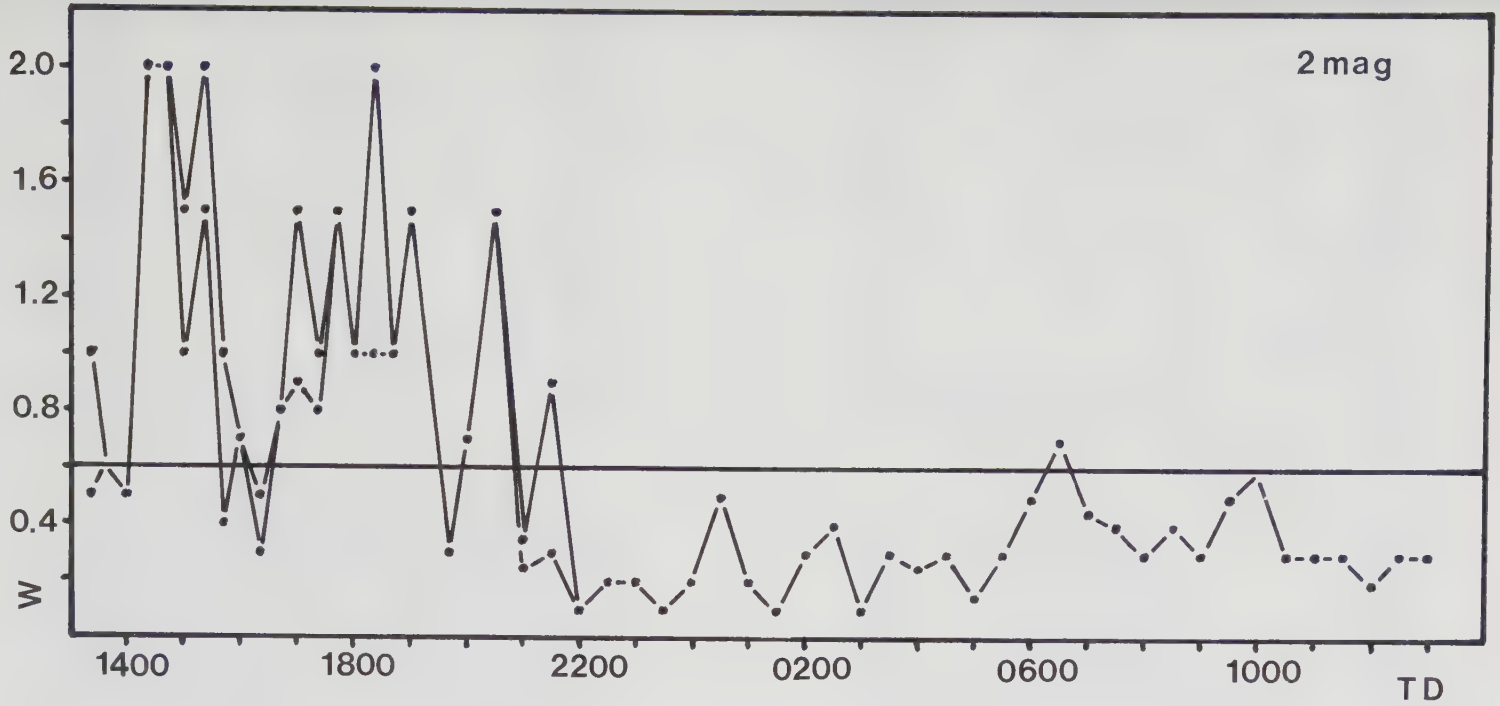


Figure 17. Deviation between the wind velocity from the mean wind velocity at Alnön in July ($\bar{W}$ 0.6) at 2 meter above ground level (cf figure 5).

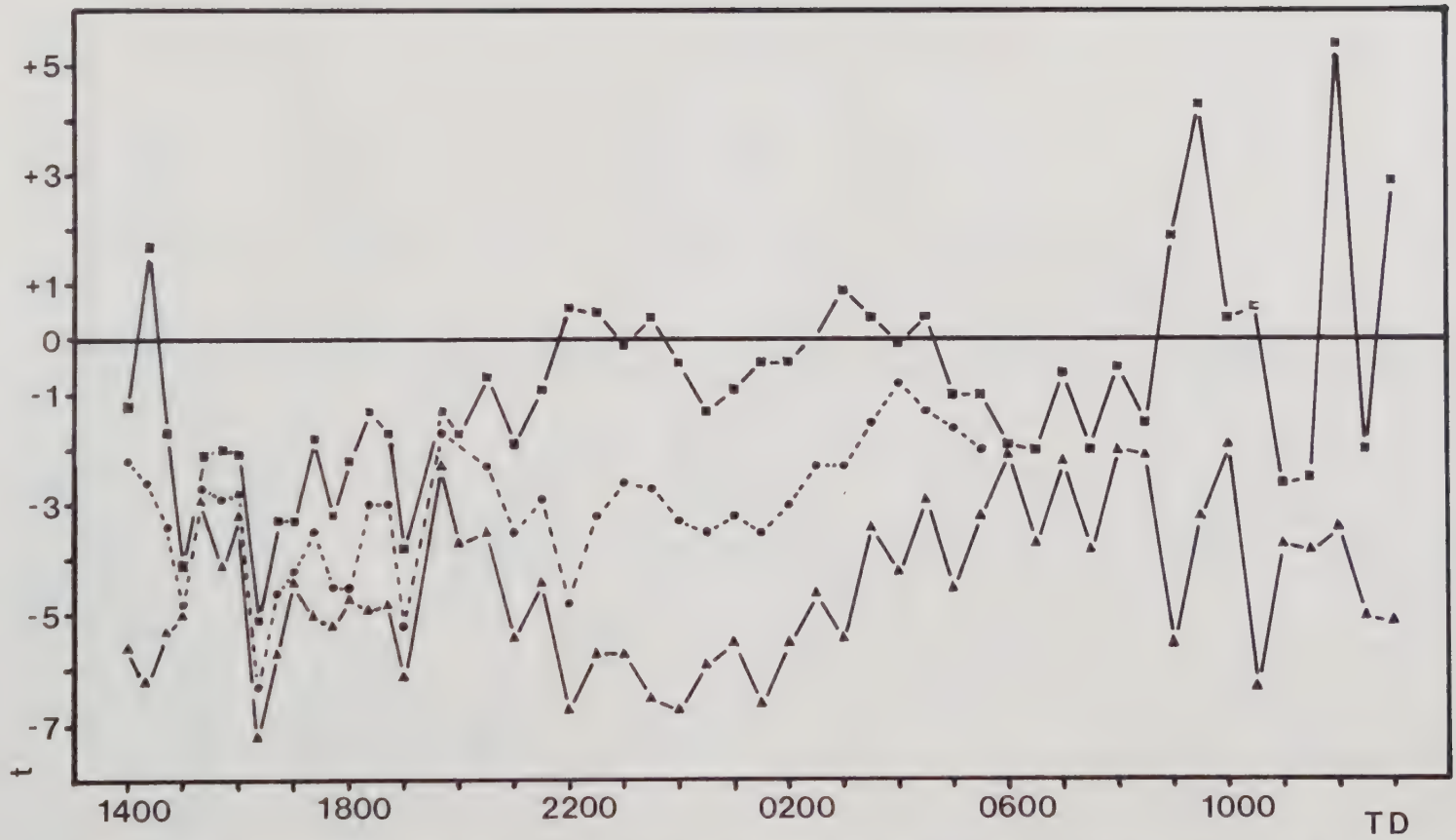
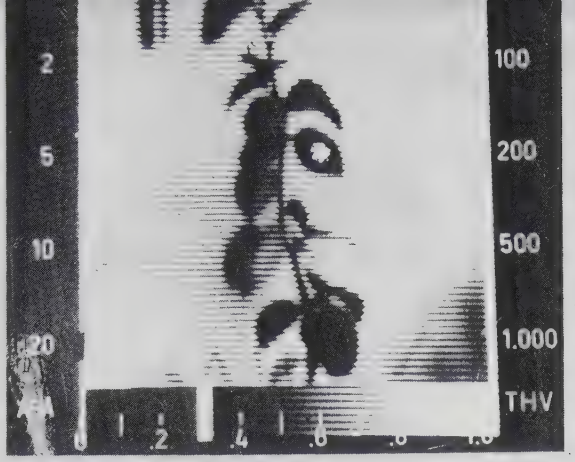


Figure 6. Deviation between the max max (■——■), min min (○----○) and diurnal (▲——▲) temperature of the birch at Alnön from the temperature of the ambient air (cf figure 5). The temperature of the birch when even (● —— ○).



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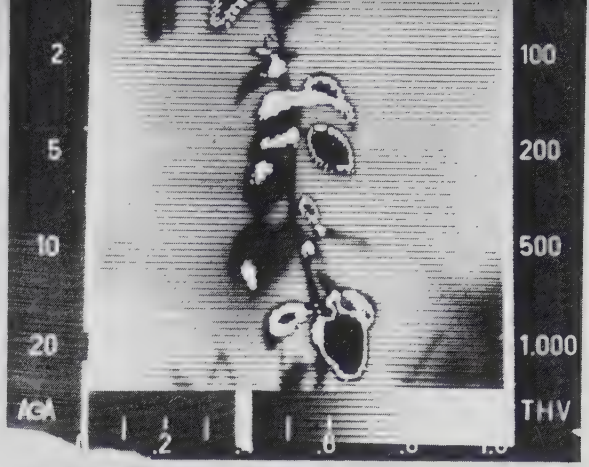

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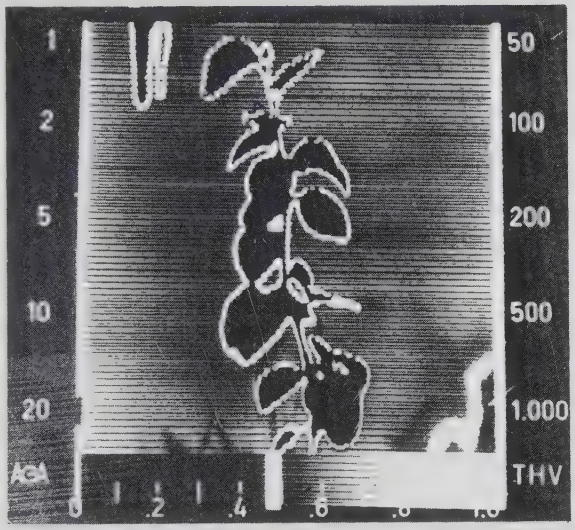

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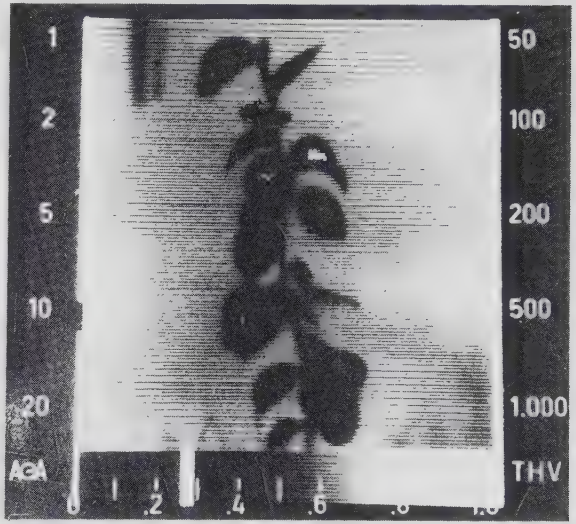

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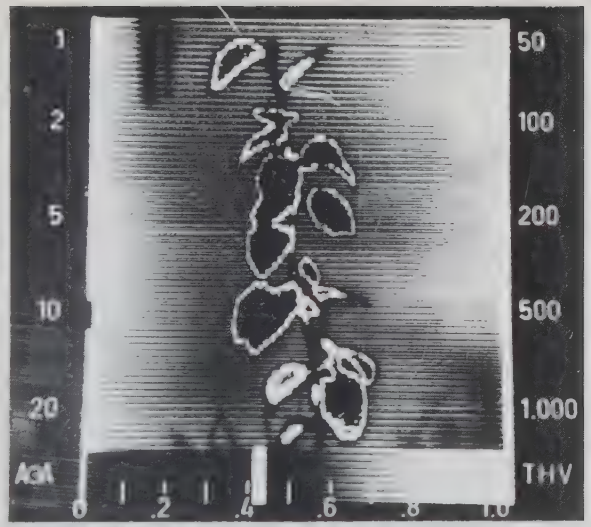
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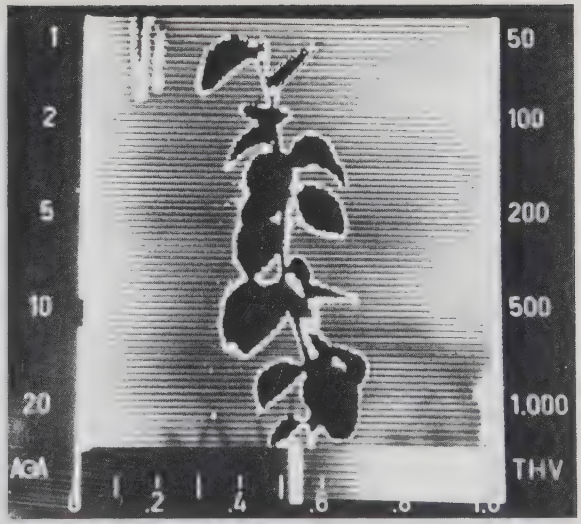
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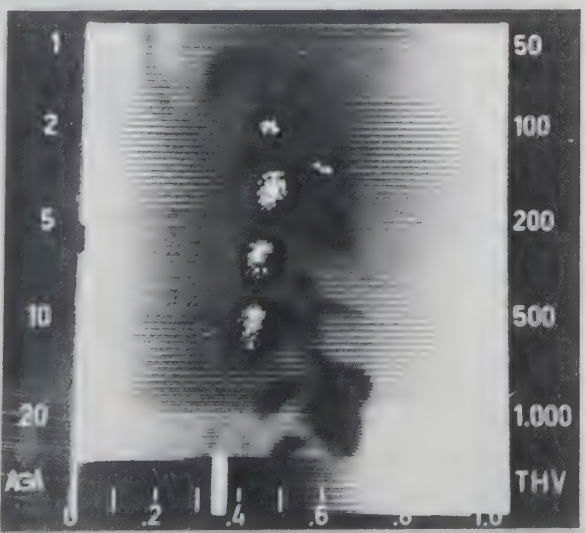
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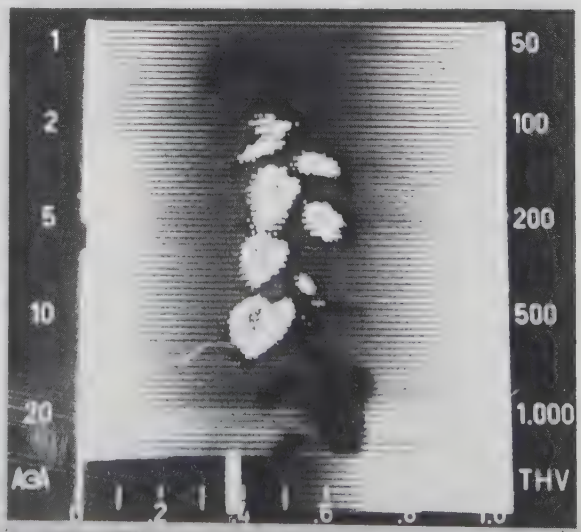
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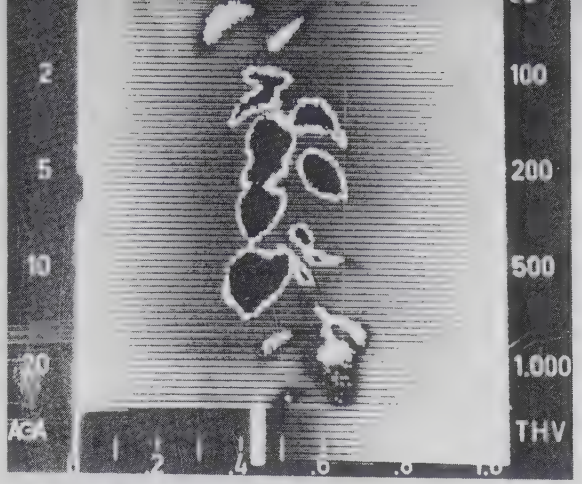

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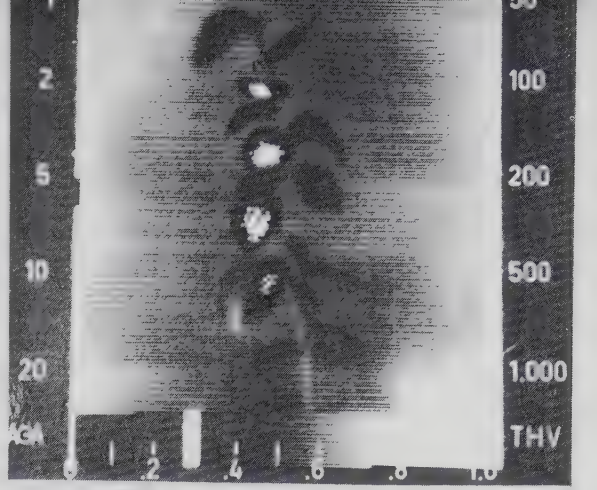

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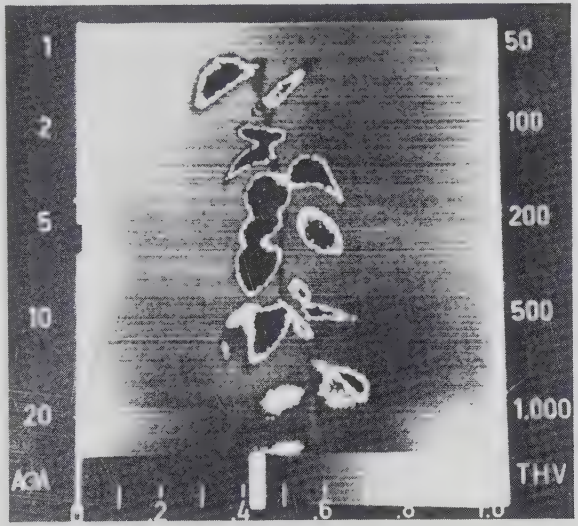

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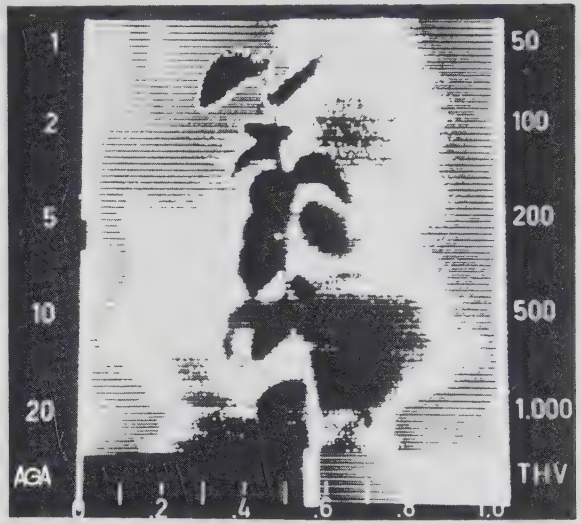

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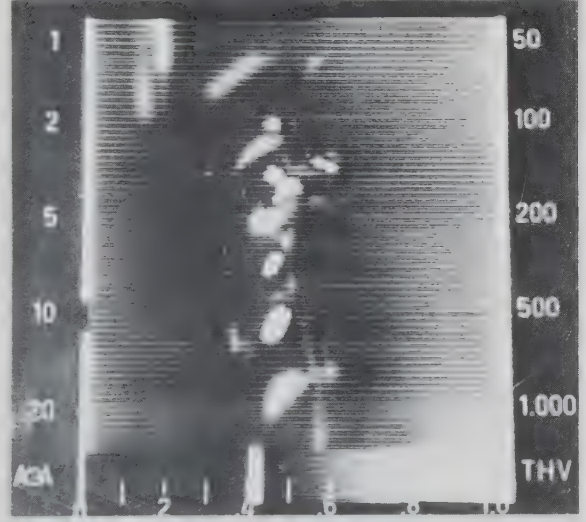
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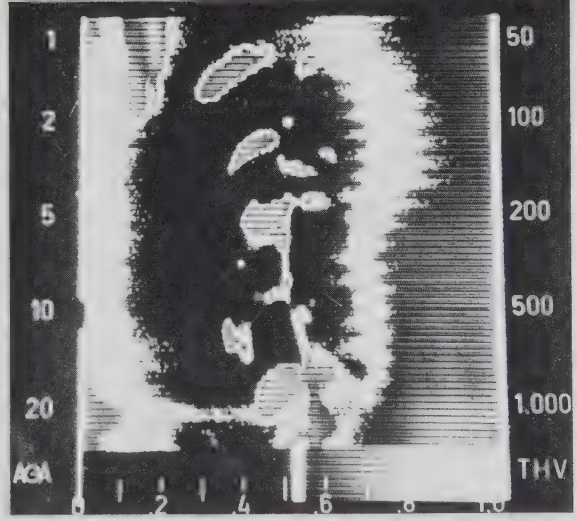
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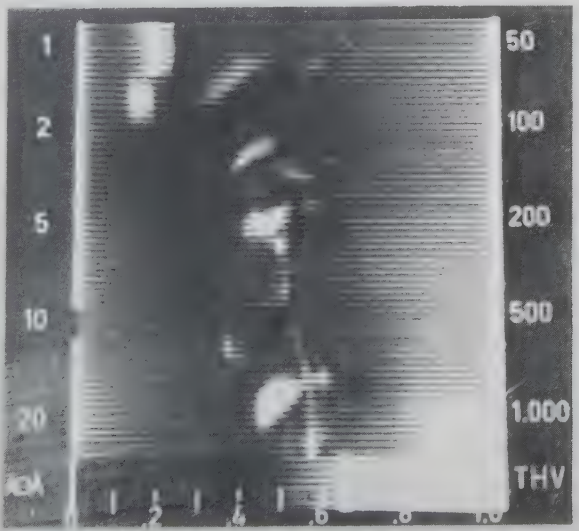
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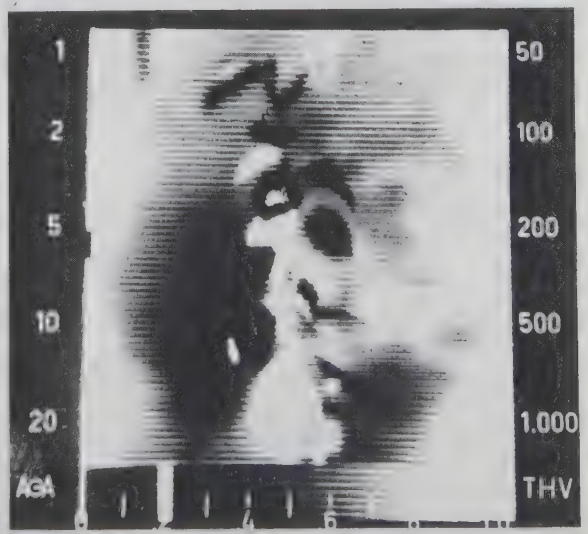
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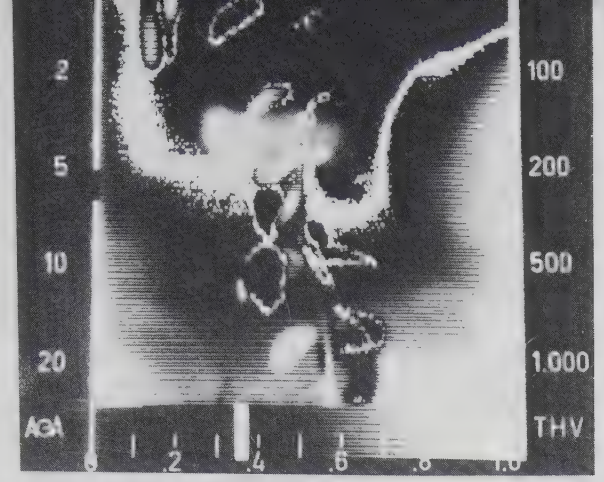

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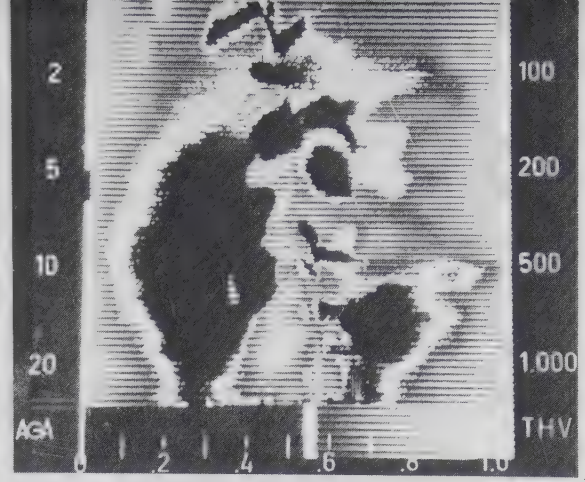

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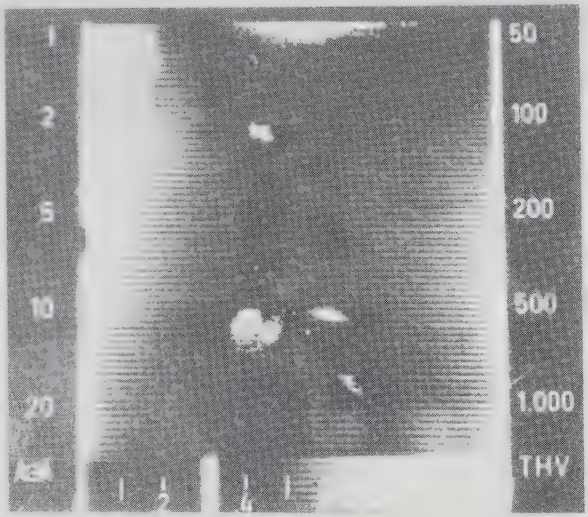

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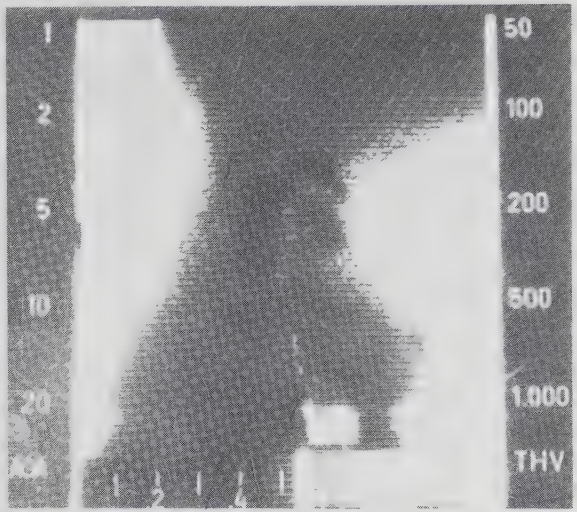

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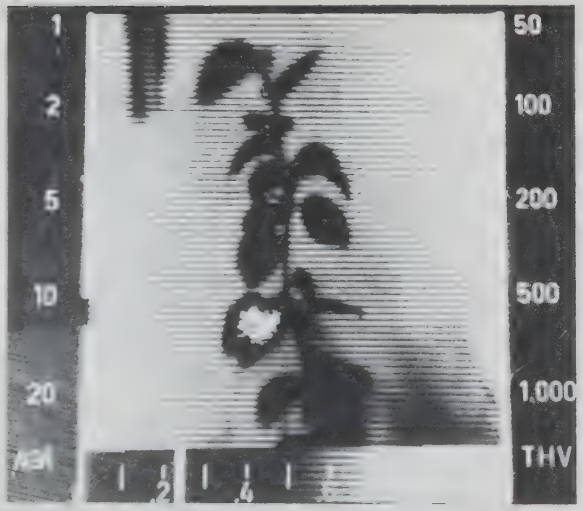

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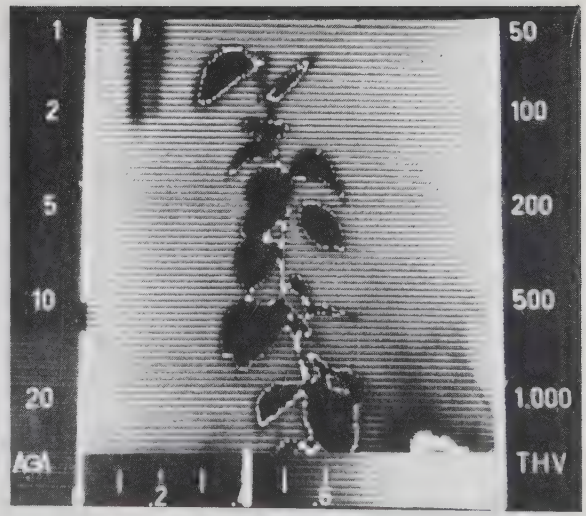

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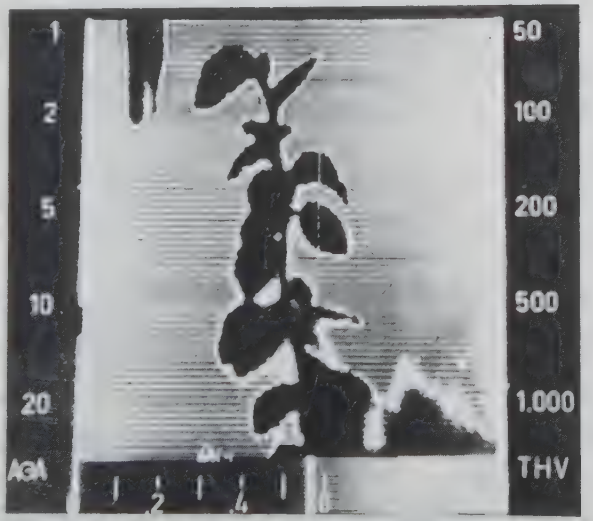

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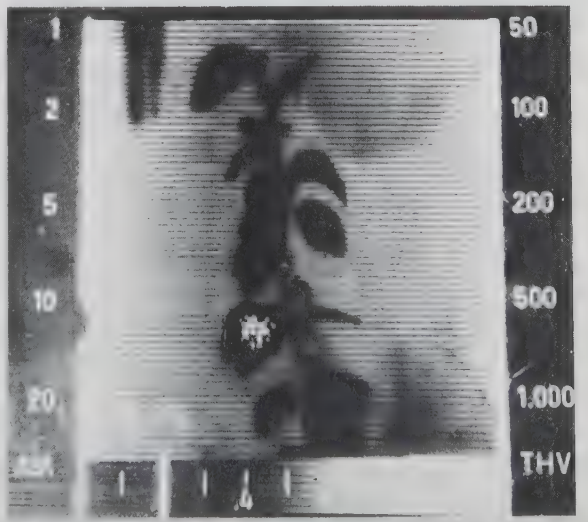

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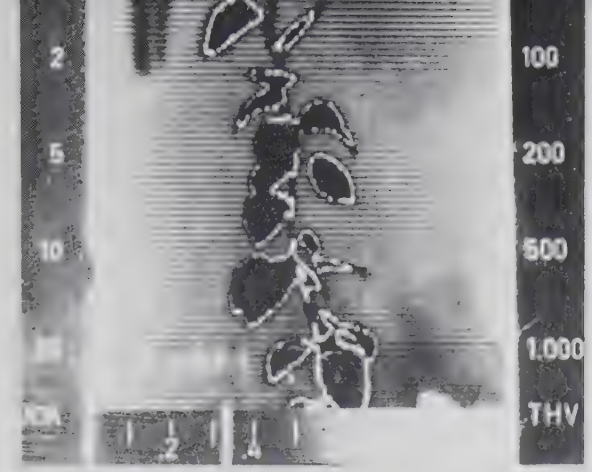
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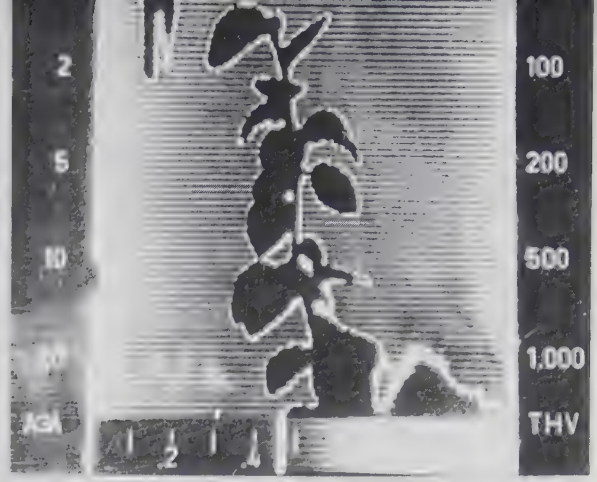
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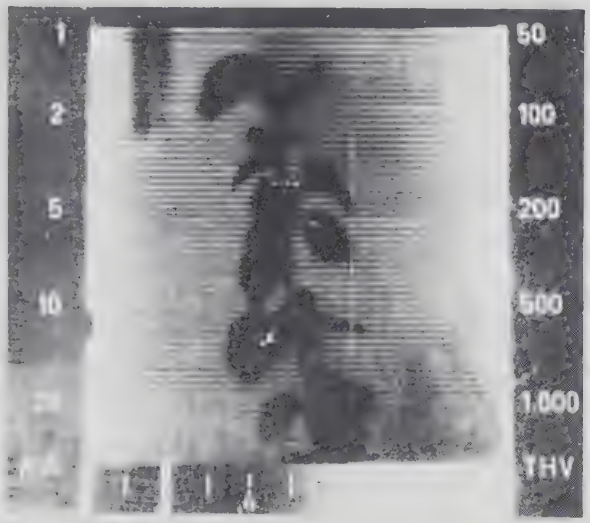
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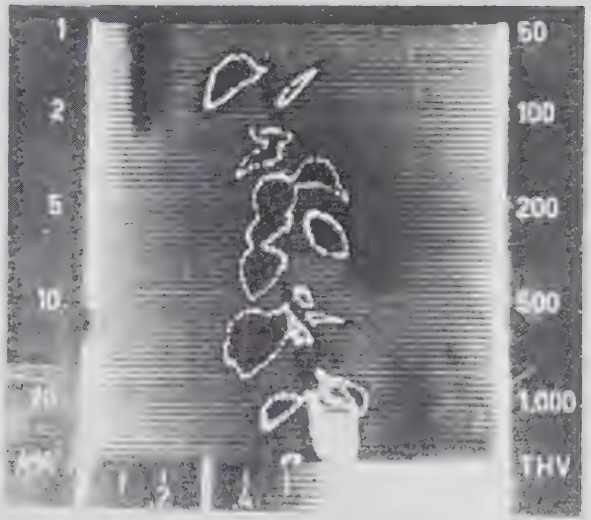
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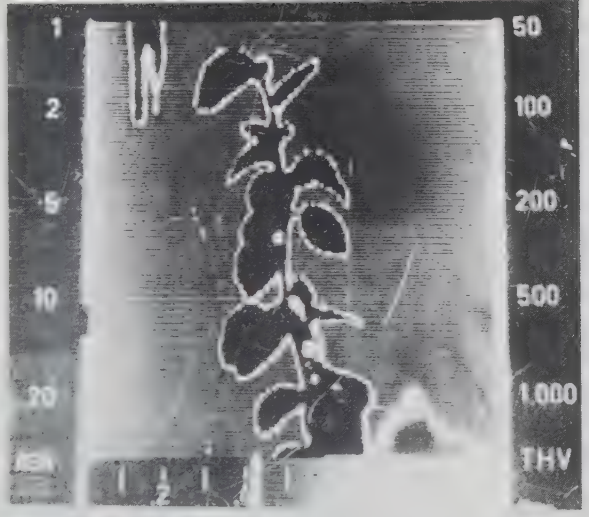

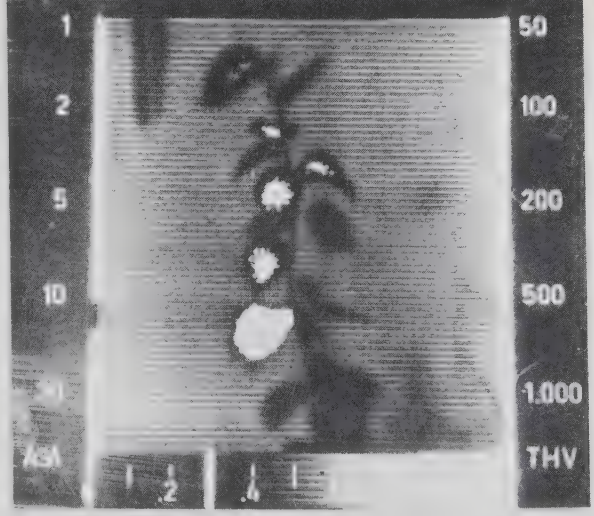

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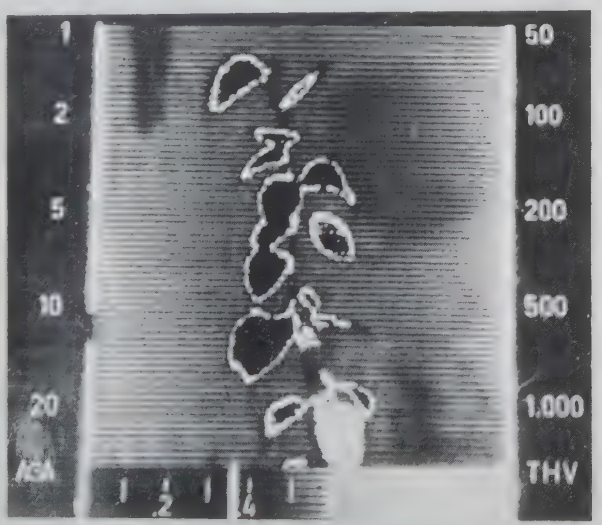

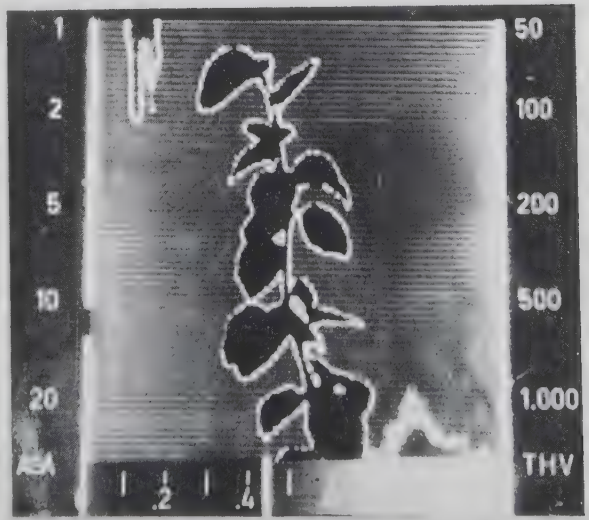

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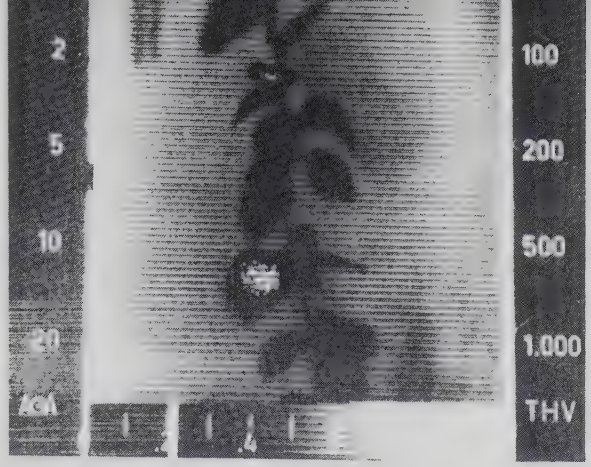

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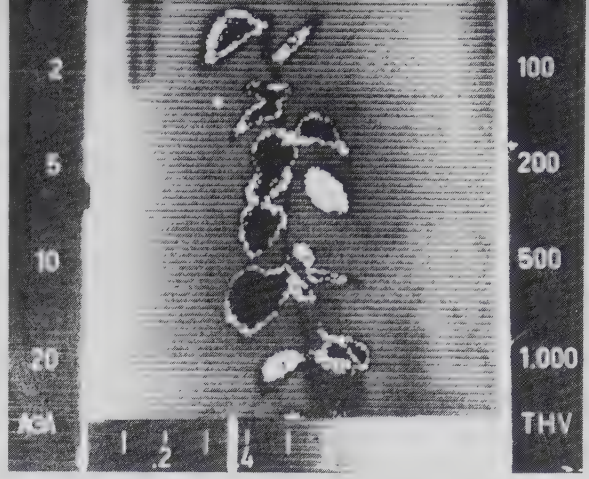

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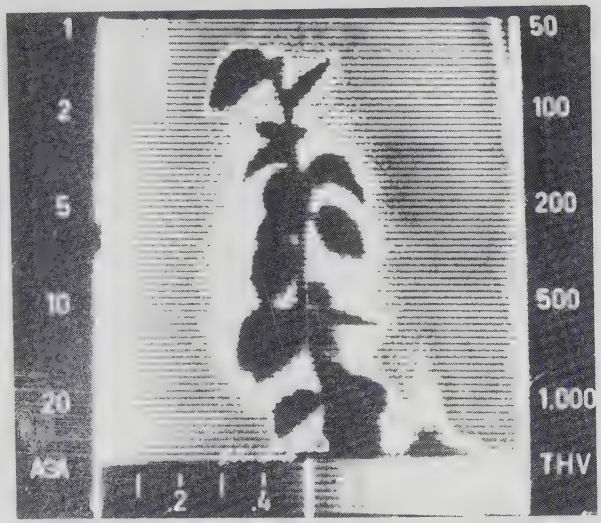

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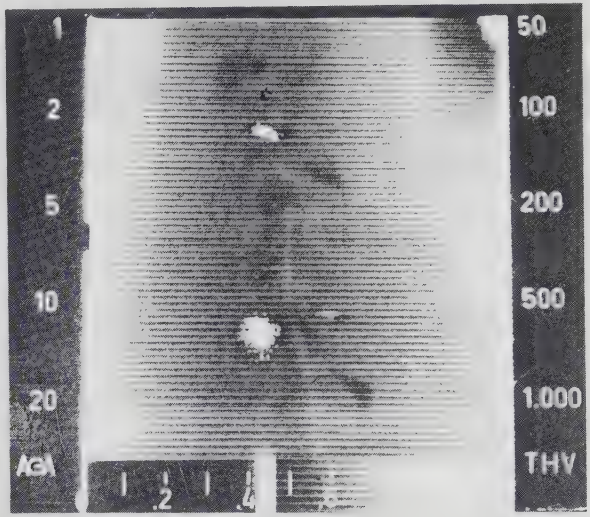

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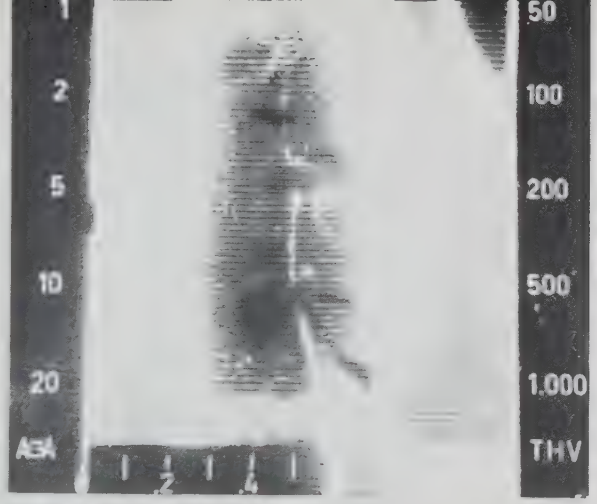
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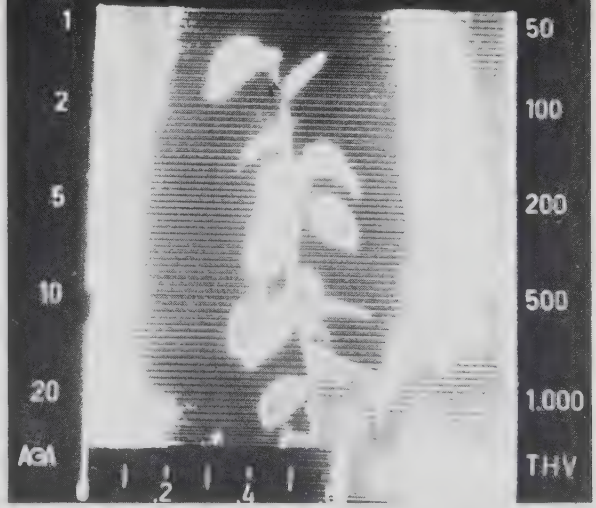
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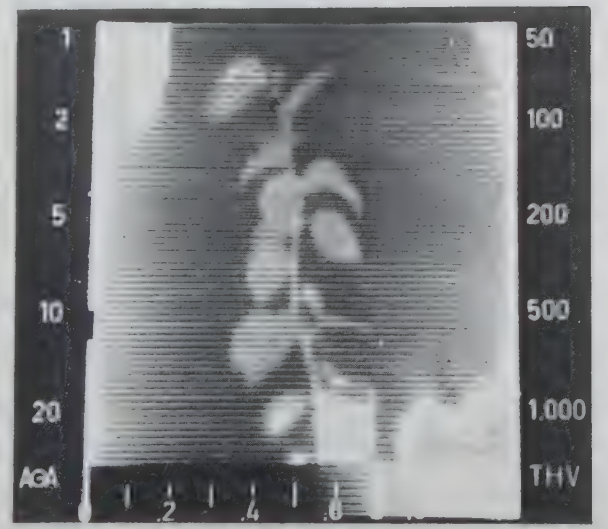
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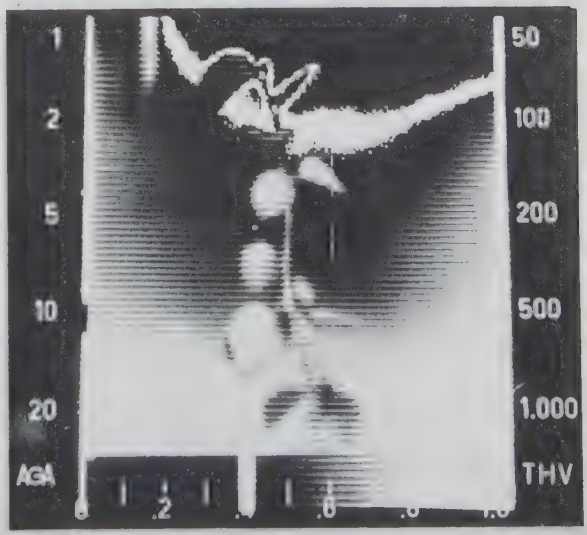
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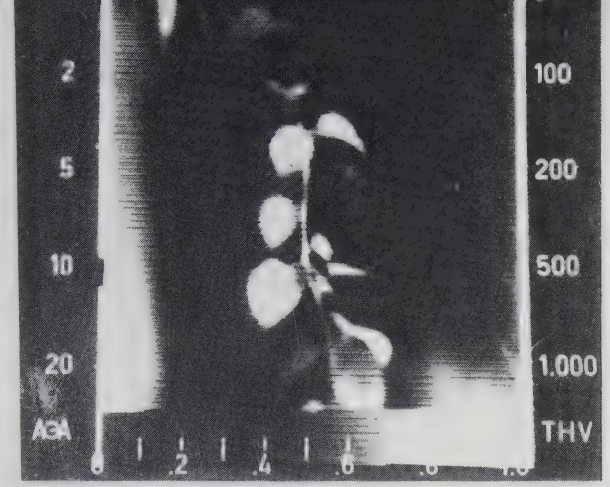

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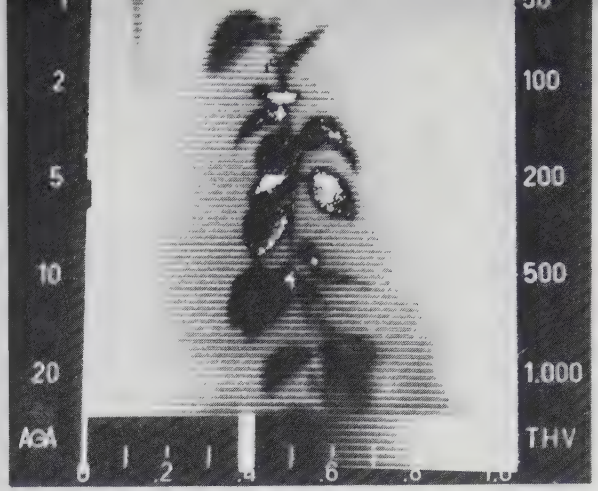

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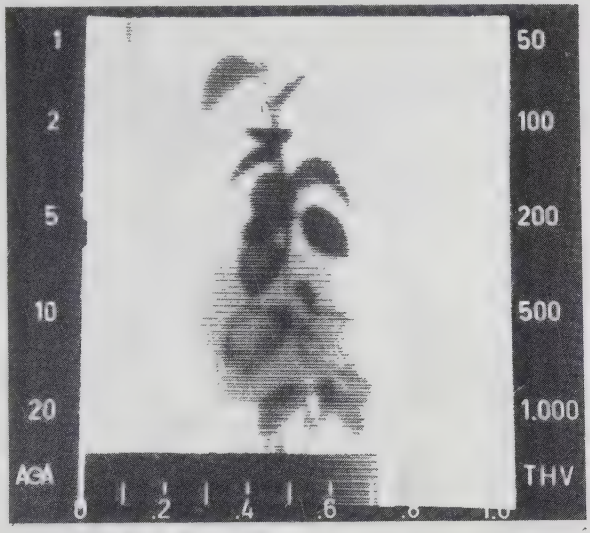

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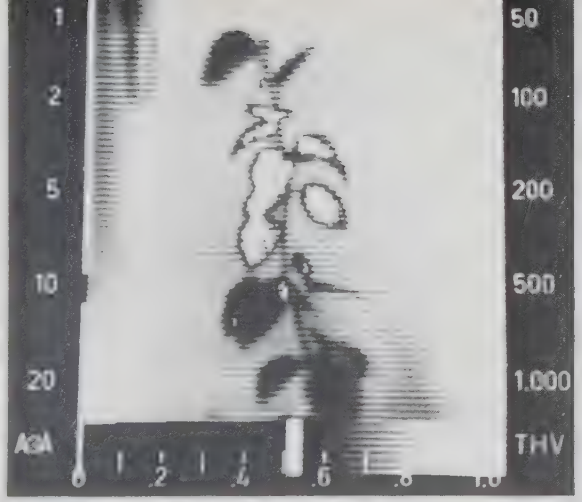
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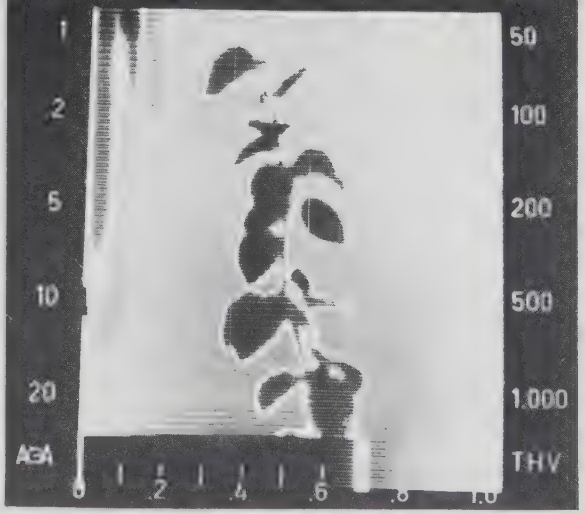
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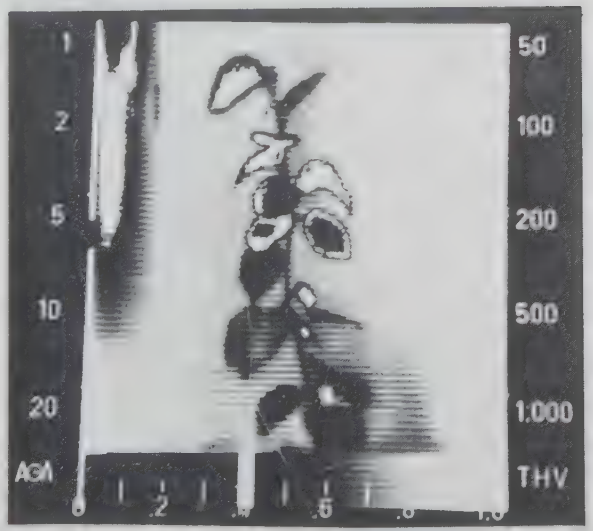
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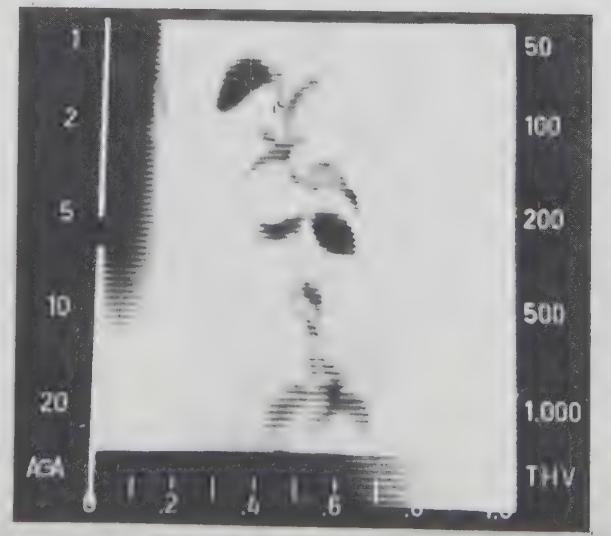
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STORHOGNA IN AUGUST.

The August weather conditions at Storhogna are shown in figures 20 to 24 and maximum, medium, and minimum temperatures of the birch in figure 25. In the damp weather, during the morning hours, the equipment did not work properly, and therefore the thermographic recordings could not start until 0830 hours. Unfortunately, the hot-wire anemometer broke down at 1500 hours.

The temperature response of the birch to radiation was less pronounced than in July. This is indicated by the distribution of the maximum temperatures during the period of high incident radiation in the forenoon (see S2:1030 to 1330 and figures 20 and 25). Note that the maxima occur at the edges of the leaf though they seem to be rather unstable judging by the "patchy" appearance of the light areas in the thermograms.

Wind seems to have little influence on the temperature of the birch. During periods of increased wind velocity (at about 1130 hours and 1400 hours) the maximum temperature was high but the minimum temperature was evidently not influenced. There was no indication that leaf position was important to leaf temperature.

Only during periods of intense radiation, was the maximum temperature above that of the ambient air (see figure 20, 25 and corresponding thermograms). When the sky was overcast, the maximum temperature was below that of the ambient air. From about 1700 hours the air was temperate, which might explain the increase in the maximum temperature from about that time. All this time, the minimum temperature was well below that of the ambient air.

In the thermograms of the afternoon and evening, the ambient air, the ground, and the birch are dark, having almost the same temperature. The temperature was falling and at 2200 hours, it began to rain. The temperature of the birch and the ground fell rapidly, like a sudden temperature avalanche. From that time on the thermal picture of the birch was very difficult to observe because its temperature and that of its surroundings were the same.

During the period of intense radiation in the forenoon, the ground was warm. The little hillock on which the birch grew was warm in the morning and cool in the afternoon and evening.

The ambient air was divided into two layers, as before (see S2:1030 to 1530). Unfortunately, the artificial thermal background

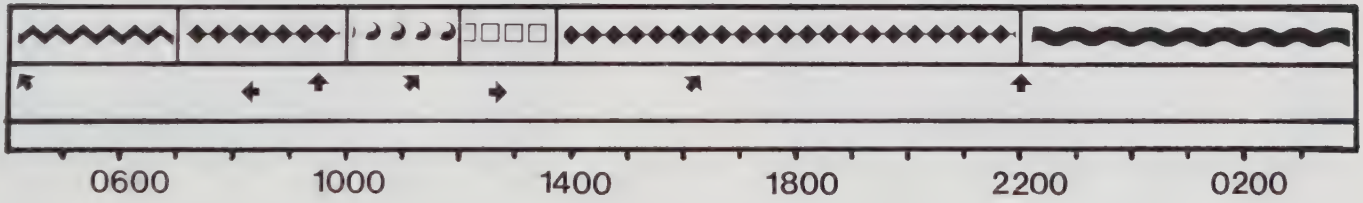


Figure 6. The predator [illegible] at Strathmore in August (cf figure 5).

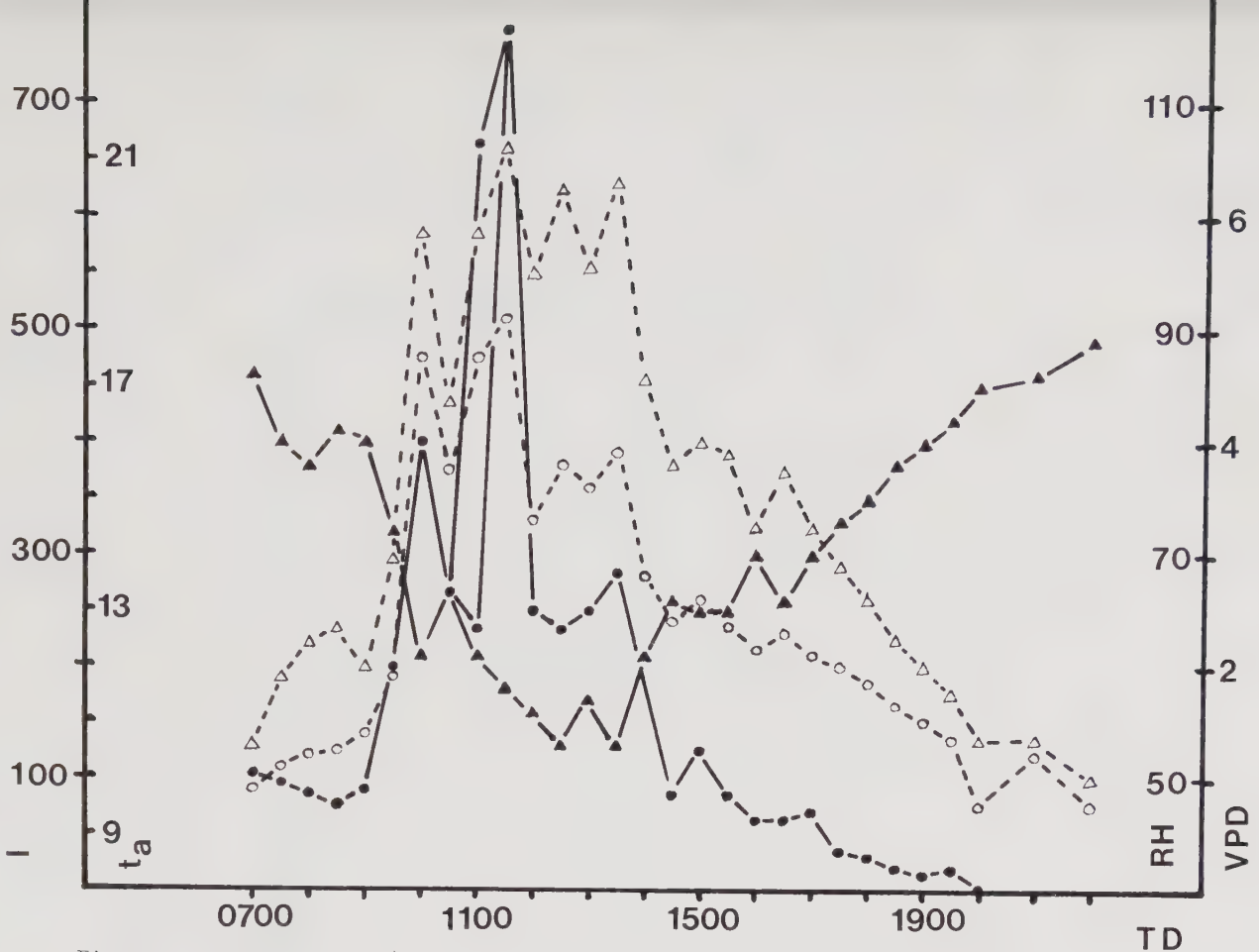
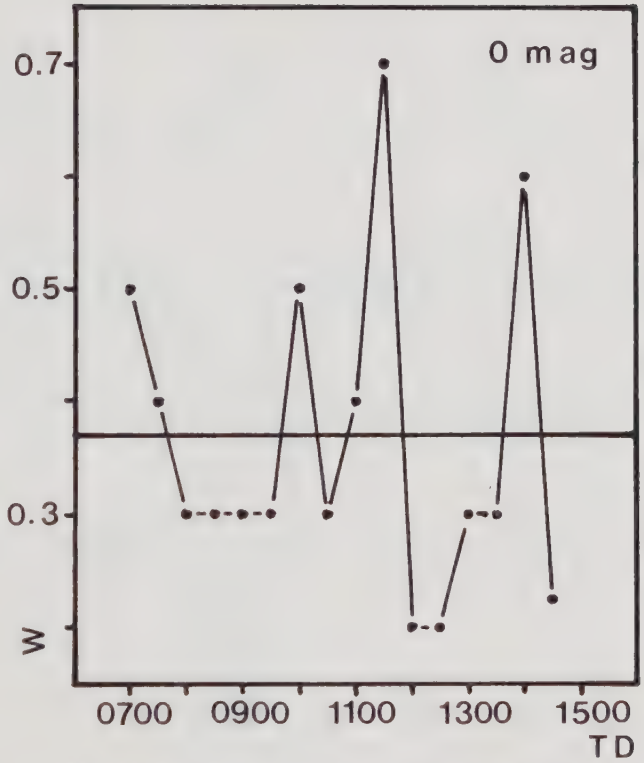


Figure 20. Changes in I (● —— ●), t_a (o----o), RH (▲ —— ▲) and VPD (△----△) during the day at Storhogna in August (cf figure 5).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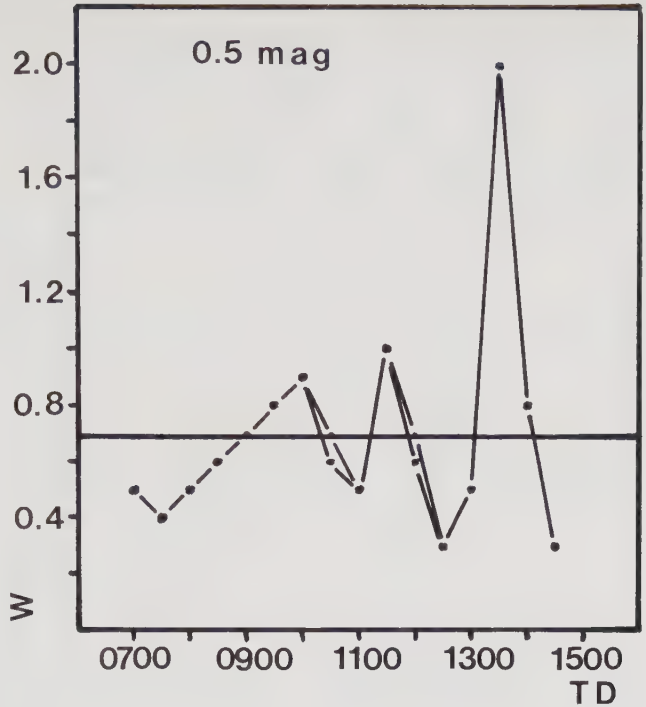
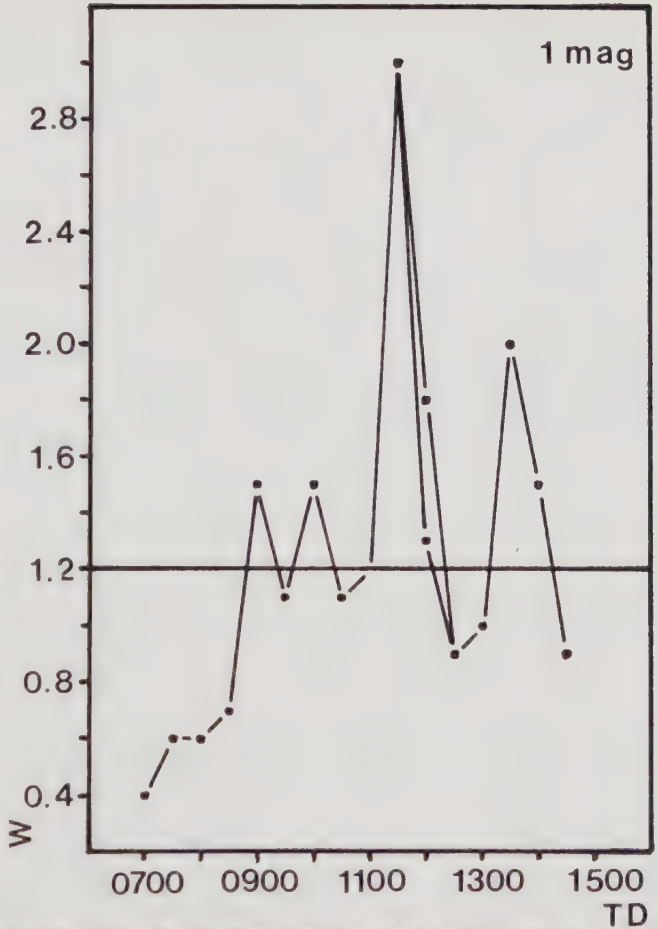


Figure 22. Deviation between the wind velocity from the mean wind velocity ($\bar{W}$ = 0.69) at 0.5 meter above ground level at Storhogna in August (cf figure 5).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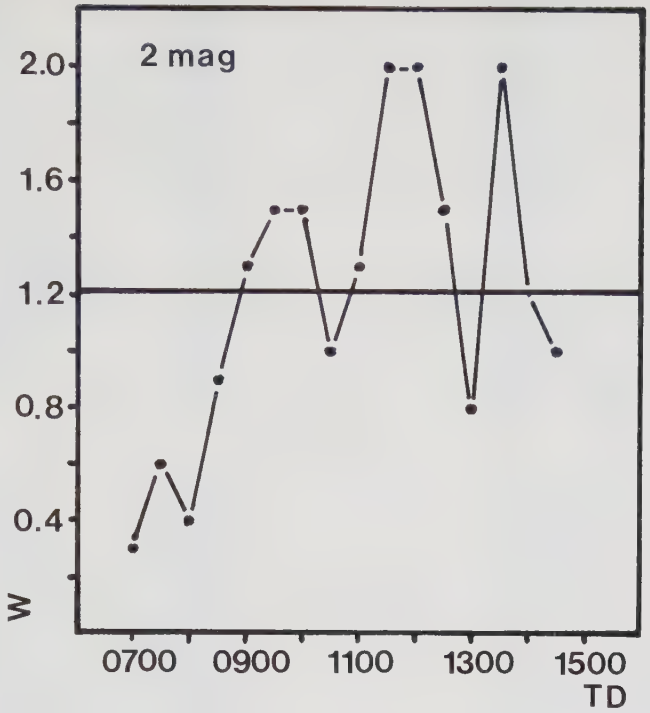
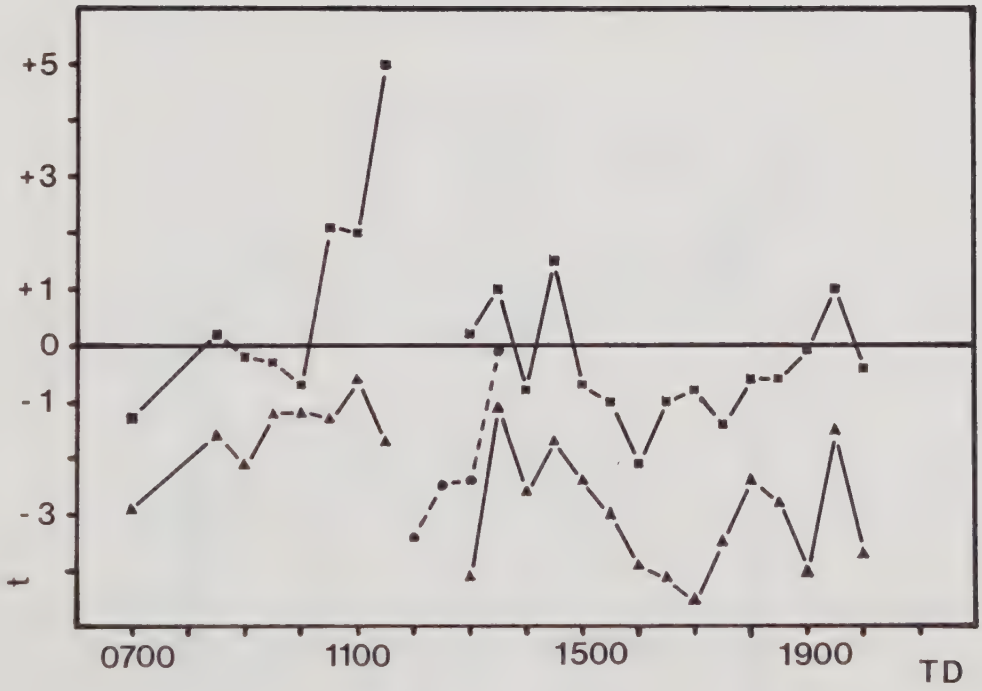
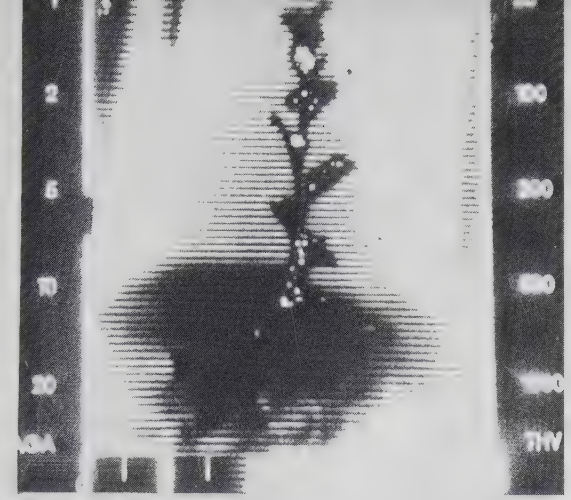


Figure 24. Deviation between the wind velocity from the mean wind velocity ($\bar{W}$ = 1.21) at 2 meter above ground level at Storhogna in August (cf figure 5).



maximum (■——■), medium (●----●) and
minimum (▲——▲) temperature of the birch at Storhogna in
August and the temperature of the ambient air. The tempera-
ture of the first week was (● —— ●).



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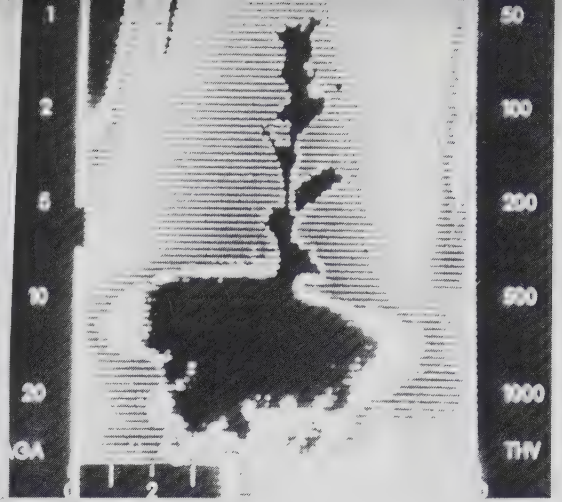

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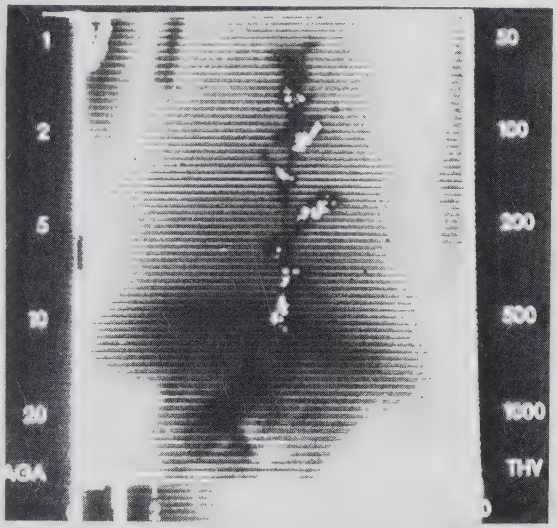

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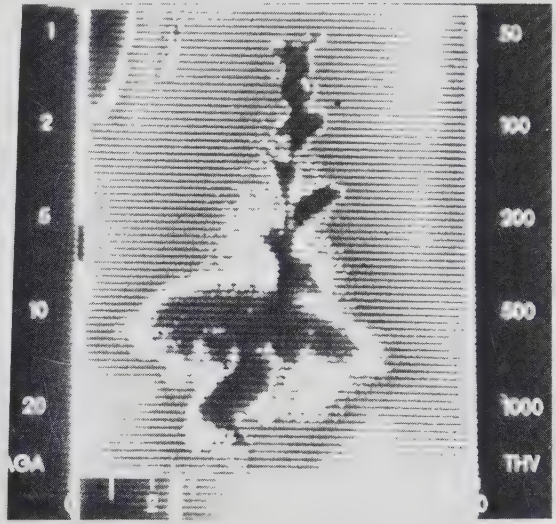

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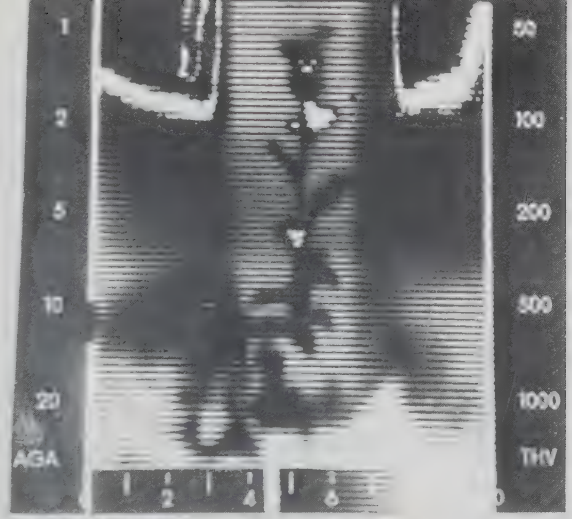

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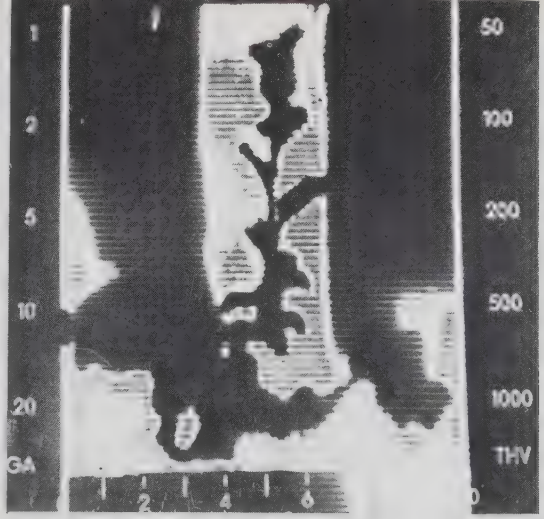

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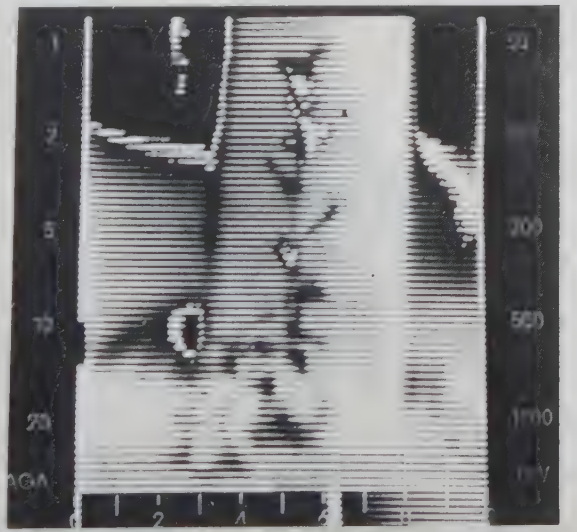

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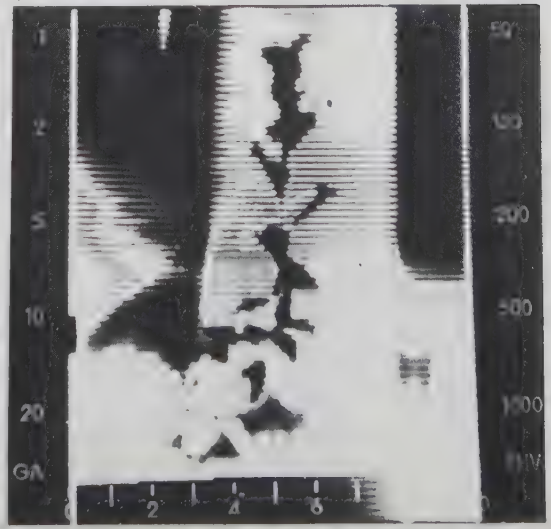

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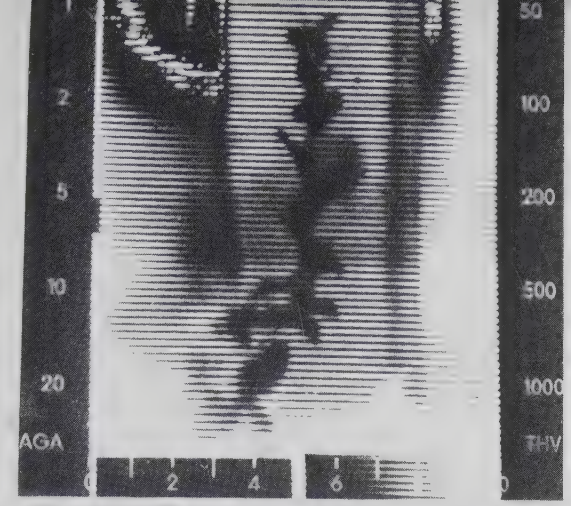

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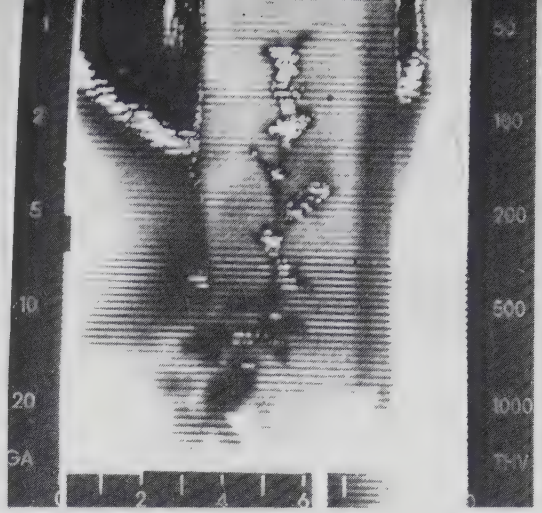

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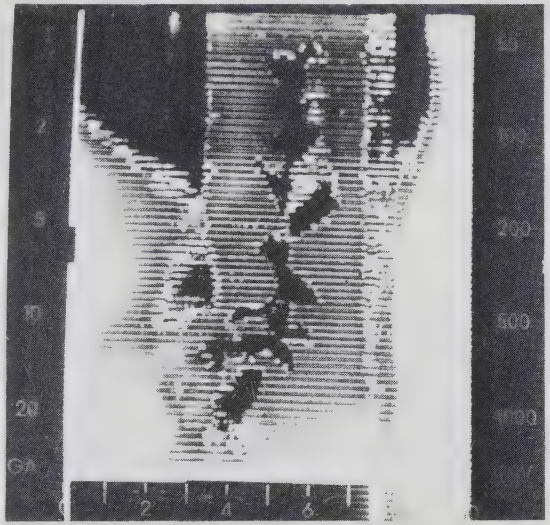

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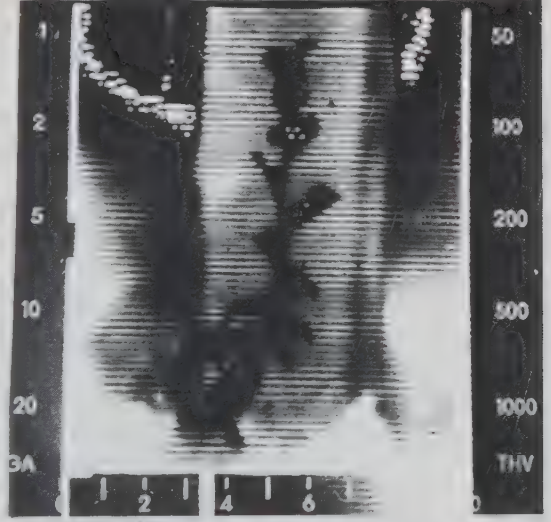
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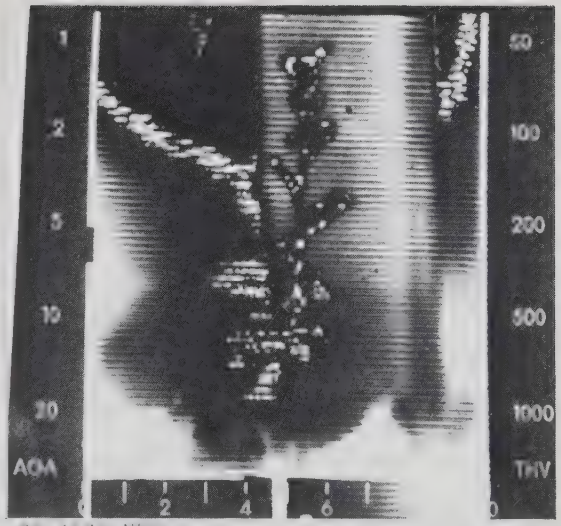
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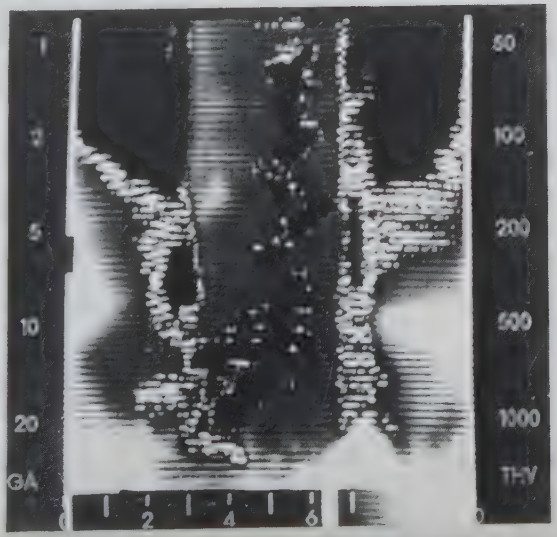
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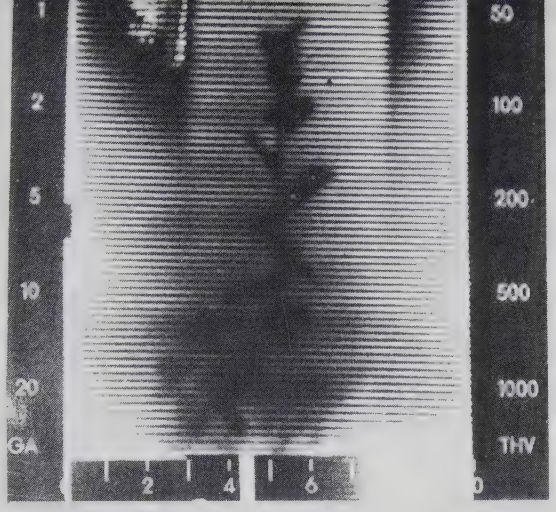

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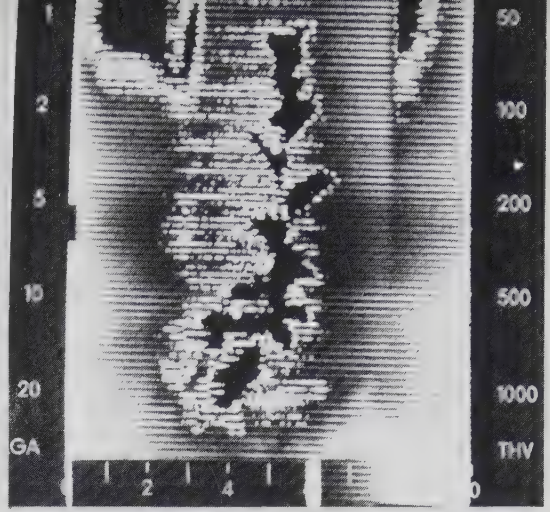

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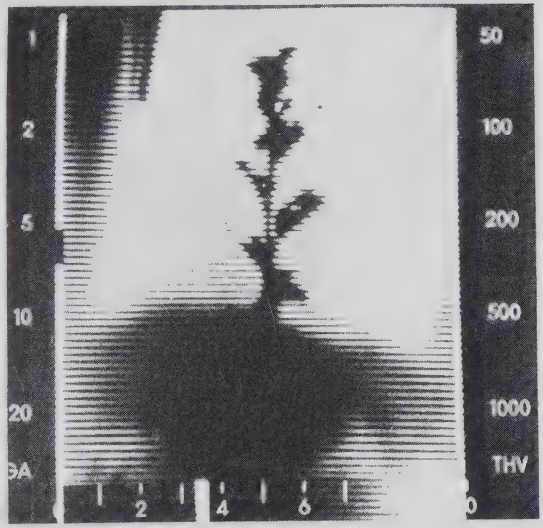

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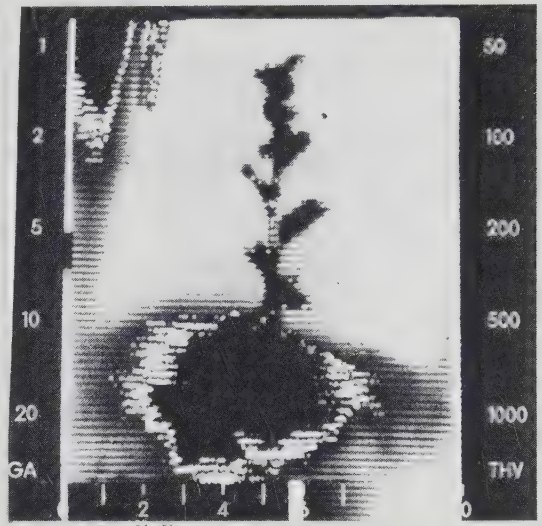

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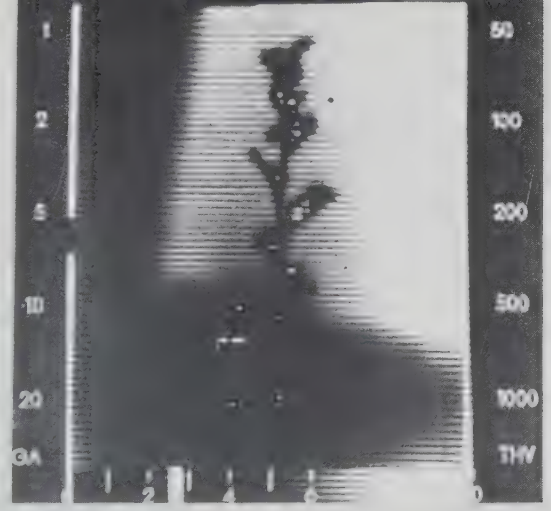

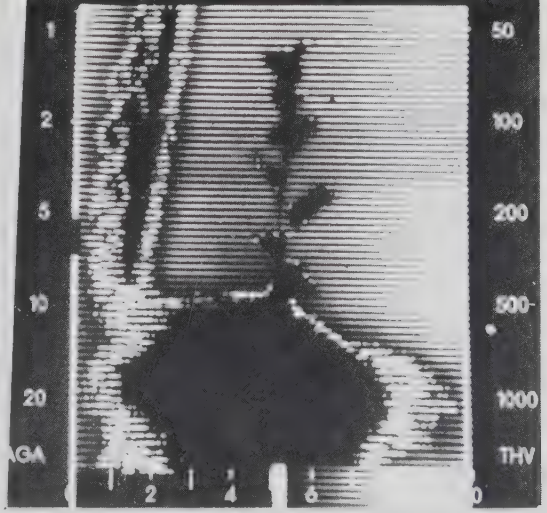

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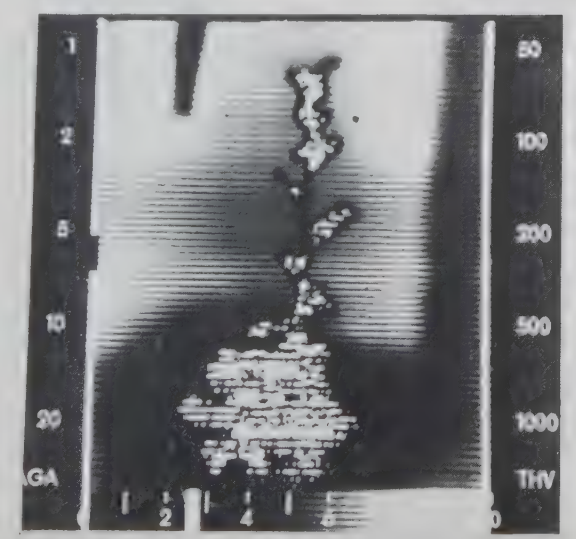

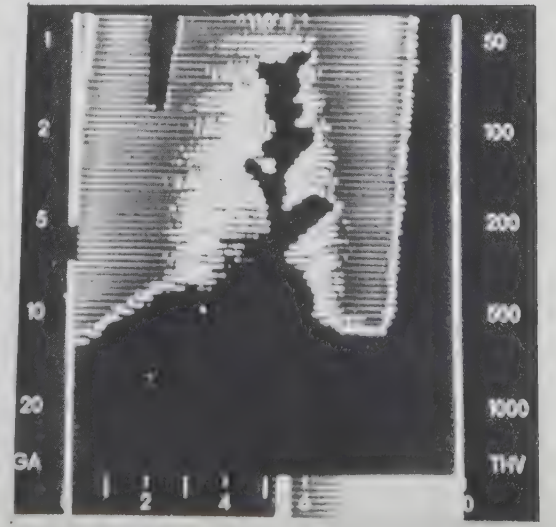

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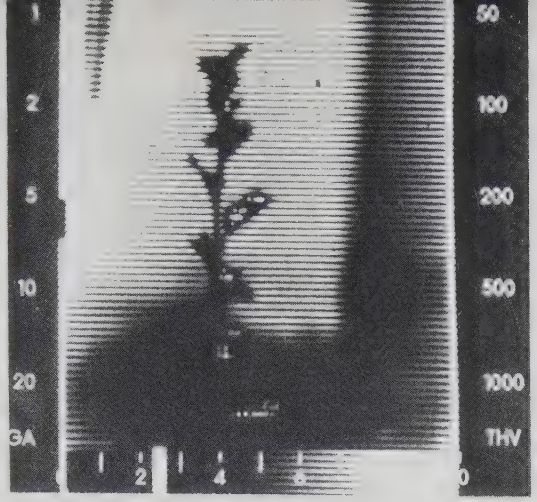

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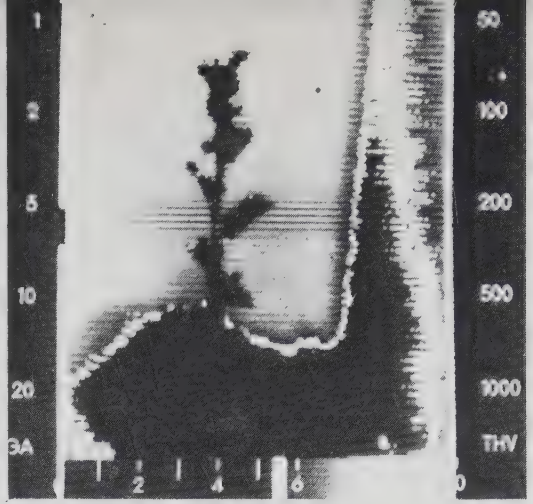

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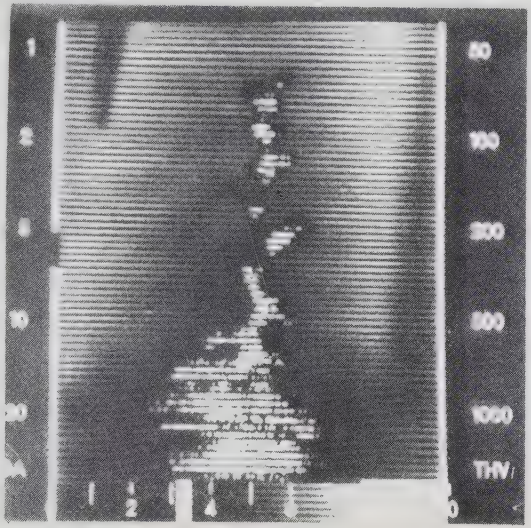

S2:2300

disturbed the thermal picture and so the two layers are not distinctly shown. The water flask served as a background from 0830 to 0930, and after 1530 (the white background in the corresponding thermograms), and the board served similarly from 0930 to 1530. By 1430 hours it was so cool as to be obscured in the thermal picture, leaving it useless as a thermal background.

DISCUSSION

The energy balance of the birch depends upon a lot of factors of which radiation, solar and terrestrial, seems to be most important. Wind, leaf position, the temperature and relative humidity of the ambient air, and the temperature of the ground also affect the energy balance.

In periods of strong insolation, the maximum temperature of the birches was well above that of the ambient air, and the difference between the maximum and minimum temperature was great. The maximum temperature is evidently always near the temperature of the ambient air and exceeds it only in periods of strong insolation. When the sky was overcast, the maximum temperature still was close to that of the ambient air. The minimum temperature of the birch was always well below that of the ambient air, except during the night at the mountain location where no differences in temperature were observed. At the mountain site reradiation from the birch was important since it loses a lot of heat through this process and is in thermal equilibrium with its surroundings, i.e. the ambient air and the ground. At sea level, the maximum temperature of the birch at night was nearly the same as that of the ambient air, while the minimum temperature was considerably lower. Here, reradiation is not effective enough to establish a thermal equilibrium between the birch and its surroundings; however, transpiration is relatively more important since a temperature gradient between different parts of the birch exists during the night.

Wind had less influence on the temperature of the birch than radiation did. The influence of wind was comparatively greater at Alnön than at Storhogna, which might be due to the more uniform moor type terrain at the mountain site and consequently, the more uniform

temperature of air transported by the wind. In the more complex structure of the terrain at Alnön, there was probably greater difference in the temperature of the air that moved past the birch, depending on the direction of the wind.

Leaf position was more important to the temperature of leaves at Alnön, than at Storhogna. Possibly, the more effective reradiation of heat from the leaves at the mountain site obscured any effect of leaf position.

The ground and the ambient air are important radiation partners to the birch. In the morning, the ground acts as a heat sink to solar radiation. As the ground warms, the heated water is conducted to the birch and warms its interior parts. In the forenoon, when the ground is warm, the birch and the ambient air near the ground begin to warm. When the ground and the ambient air is cool, the birch is also cool. Consequently, the temperature of the surroundings are important to the temperature of the birch. Reradiation balance determines the temperature of the birch, that is, as long as the surroundings are cooler, then the birch loses heat and its temperature is low but when the surroundings are warm, they reradiate heat to the birch, increasing its temperature. When solar radiation is intense and the surroundings are warm, the temperature of the birch is increased by absorbed solar radiation and reradiation from its thermal neighbors. Only transpiration and convection (wind) reduce the temperature level but are not adequate to counteract the temperature increasing effects of radiation.

Reradiation from the air to the birch is also an important source of heat. When the sky was overcast, as for instance, the afternoon at Storhogna in August, the maximum temperature of the birch was about the same as that of the ambient air, but the minimum temperature was below that of the ambient air. The indirect radiation supplied enough heat to establish a temperature gradient in the birch.

During the day a stable air layer near the ground exists which is more stable in clear, calm weather, than when the sky is overcast. The lower part of the birch was found in that warm air layer, the upper half in the cooler and presumably more turbulent air layer

(Storhogna in July) thus the lower half of the birch had a radiation partner more warm and stable than the upper half. The transition zone between these two air layers determines the heat flow from the lower to the upper air layer. This is shown by the fact that the leaf situated exactly in the border zone (leaf B in figure 1) was the coolest during the day. It was especially evident in the afternoon when wind velocities increased (about 1500 hours). Here convection of heat plays the important role in transferring heat from the leaf.

In the evening and night heat is lost by reradiation, but is counteracted to a certain degree by the conduction of warm water from the ground into the birch. At Storhogna in August, it was observed at 2200 hours that an area about the same diameter as the height of the birch, was distinctly cooler than the ground farther away. The heated water from this cooler area must have been conducted through the birch then lost by transpiration. The ground presumably stores heat and supplies warm water to the birch during the evening and first part of the night.

During the night at Alnön, the broad leaves to the left in the thermograms were warm, but the grass leaves to the right, growing on a small tussock, were cool. Presumably the broad grass leaves were transpiring more, due perhaps to a stronger root pumping mechanism, than the narrow, rounded leaves of the grass growing on the tussock, or the temperature of the leaves might have been lower because of more effective reradiation (cf Tibbals et al 1964).

The influence of rain water was dramatically shown in the evening at Storhogna in August. This was an example of water as an external environmental factor influencing very effectively the temperature of the birch. As a rule, the temperature of a plant is reduced by rain water because it is cooler than the plant.

Thermography gives an excellent thermal picture of a plant and its surroundings (Thofelt 1975 b). However, there are some complications in using it especially concerning the true temperature of an object and its surroundings.

Relative temperature differences between objects in a thermal picture must be of considerable magnitude if the object of interest, the plant, is to be distinguished from the ambient air, the ground, and the background. This problem was solved by using different types of artificial thermal backgrounds: a screen made of corru-

gated paper (used shortly at Alnön), a board, and a water-flask. However, these devices disturbed the thermal surroundings, especially the air layers near the birch. The disturbances were more pronounced at Storhogna in August than in July or at Alnön. The board disturbed the thermal surroundings much less than the water-flask. Presumably, in cold, damp, cloudy weather, with only a short period of direct radiation from the sun, the water-flask with its thermal capacity dominated the thermal picture. To eliminate this problem the measuring procedure can be changed. The temperature of the ambient air, and the maximum and minimum temperature of the plant would need to be measured. The temperature of the ambient air could be supplemented with some thermograms at temperatures one or more degrees Celsius above and below that of the ambient air, depending on the thermal conditions of the object and its surroundings. The thermal picture of the ambient air, the plant, and the ground with other objects near of the plant could in this way be documented. A similar procedure could be followed when recording the temperature of a plant. The maximum and minimum temperatures of the plant could be measured and recorded with thermograms and complemented with thermograms of intermediate temperatures between the maximum and minimum. The thermal picture or the thermal details of a plant could be adequately measured and documented by this stepwise temperature recording of the different temperature gradients of the plant and its thermal neighbors. In periods of changing weather conditions with large temperature differences of the plant and its surroundings, the documentations system could advantageously be supplemented with a video-tape recorder (cf Thofelt 1975 b).

An additional complicating factor in measurements of the true temperature of plants is its reflectivity (Thofelt 1975 b). Reflectivity is dependent upon the water content and structure of the leaves, at least in the wave-length band up to 2.6 µm (Hoffer and Johanssen 1969, Sinclair et al 1971). In the infrared reflectivity of leaves is about 5 % (Wong and Blevin 1967). To be able to measure the exact true temperature of leaves during a day, it might be necessary to know the water content of the leaves and the plant parts, especially for periods of strong insolation on still, hot days. The water content of the leaves could then be correlated to reflectivity values of leaves at different levels of water content

determined in the laboratory. However, the difference in reflectivity of live decidous leaves of varying water saturation in the infrared wave-lengths measured by the THV, may not be of practical significance in the field.

The procedure of measuring the temperature of leaves at different heights of the plant as was done at Storhogna in July, is not recommended because it was found that the leaves did not represent the thermal patterns of the plant.

THV measurements for true leaf temperatures can not be exact with the now existing techniques; on the other hand, no other technique can be either (cf Thofelt 1975 b). In ecophysiological studies, the changes in temperature and temperature differences of the object are more interesting than an exact knowledge of the true temperature level. Here thermography (THV 680) is an excellent method of measurement, especially for short time measurements.

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ACKNOWLEDGEMENTS

At the Institute of Physiological Botany, Professor Nils Fries in 1964 created a possibility for students to do most of their research outside the walls of the institute. This gave me the possibility to continue my teaching work in Östersund, Jämtland, simultaneously with my doctorial studies. Without this arrangement, this investigation would never have been done. I wish to sincerely thank Professor Nils Fries for this possibility and for encouraging support and interest during the past years.

To my teacher Dr. Henry Rufelt, I am deeply indebted. He has introduced me into the problem which is an extension of his own studies on water relations and productivity of forest trees. I should also thank him for allowing me to use the equipment of his group. During the work, he has given many valuable suggestions and in all possible ways helped to put this work through.

The thermographic studies were made possible by a joint grant from the Swedish Natural Science Research Council.

Stig Lindell and Björn Åke Wiik, El & Termokonsult AB, Sundsvall, kindly and generously placed their technical skill and the THV equipment to my disposal. They supported the work in every way possible, both in the laboratory and in the field, helping to make it a reality. I am deeply indebted to them for many valuable discussions and friendly assistance. I also want to thank Jan Olof Olsson, El & Termokonsult AB, for helpful assistance in the determination of some characteristics of the leaf.

The equipment used in measuring the leaf temperature by the repeated touch method and incoming radiation was constructed by Bertil Örn, AB Instrumentplast, Östersund, to whom I express my sincere gratitude.

Most of the scientific articles necessary for the work were brought into my hands by Margareta Körlof, Jämtlands Läns Bibliotek, Östersund, whose skilful assistance enabled a thorough grasp of the literature concerning leaf temperature. I am very grateful for her competent help during the past years.

For help with the transpiration measurements and for technological assistance I especially want to thank Jan Parsby, Institute for Physiological Botany.

My English text was thoroughly revised by Solveig Pearson and Prof. Lorentz Pearson, to whom I express my deep gratitude.

Russian texts have been translated by Leif Sahlgren, Östersund, whose help has been most valuable.

The thermograms were reproduced by the photographic skill of Lars Rosengren, City-Foto, Östersund. I am very grateful for all his help.

The manuscript was typed and put into shape by Inga-Britt Jansson, which I gratefully acknowledge.

All friends, at the institute and at school, I want to thank for encouraging support during the past years.

As for my family, I hope the future will be better than the past.

The work was supported by the Institute of Physiological Botany, Uppsala, The Swedish Natural Science Research Council, The Swedish Council for Forestry and Agriculture Research, and "Stiftelsen Carl och Nanna Bodmans Efterkommande"-fund, which I gratefully acknowledge.

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ISBN 91-554-0341-7

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